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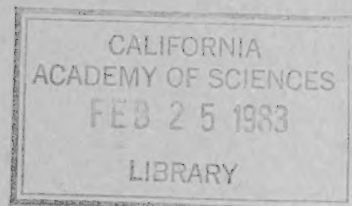
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# The Systematics and Distributional Ecology of the family Ampeliscidae (Amphipoda: Gammaridea) in the Northeastern Pacific Region I. The genus *Ampelisca*

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## ABSTRACT

The genus *Ampelisca* is represented by 14 species on the North American continental shelf in the region between the Bering Sea and Northern California. Taxonomic analysis of the extensive collections in the Canadian National Museum of Natural Sciences extends the ranges of nine species from Oregon or California to northern British Columbia or southeast Alaska. Three species are recorded from near St. Lawrence Island in the Bering Sea. A new species *Ampelisca hessleri* is described from northern British Columbia waters. A bathymetric subspecies *Ampelisca macrocephala unsocalae* Barnard 1960 is elevated to species rank. Two geographic variants are elevated to separate species: *Ampelisca fageri* from *A. schellenbergi* Shoemaker 1933; *Ampelisca careyi* from *A. macrocephala* Liljeborg 1852. A key to the genus for the northeast Pacific region is included. A cluster analysis is performed on the northeast Pacific *Ampelisca* fauna. Sub-generic phyletic relationships are pointed out, but no attempt is made to divide the genus *Ampelisca* due to the mosaic distribution of characters among the species.

## RÉSUMÉ

Le genre *Ampelisca* est représenté par quatorze espèces sur le plateau continental nord-américain, dans la région qui s'étend de la mer de Béring au Nord de la Californie. L'analyse taxinomique des vastes collections du Musée national des sciences naturelles du Canada permet d'attribuer à neuf espèces un territoire plus grand, qui s'étend de l'Oregon ou de la Californie au nord de la Colombie-Britannique ou au sud-est de l'Alaska. Trois espèces provenant du voisinage de l'île Saint-Laurent, dans la mer de Béring, sont signalées. Une nouvelle espèce, provenant des eaux septentrionales de la Colombie-Britannique est décrite : *Ampelisca hessleri*. Une sous-espèce bathymétrique est reconnue comme espèce distincte : *Ampelisca macrocephala unsocalae* Barnard 1960. Deux variantes géographiques sont aussi reconnues comme espèces distinctes : *Ampelisca fageri* (précédemment *A. schellenbergi* Shoemaker 1933) et *A. careyi* (précédemment *A. macrocephala* Liljeborg 1852). L'auteur fournit une clé des espèces appartenant à ce genre dans le nord-est du Pacifique et une analyse par populations des espèces d'*Ampelisca* du nord-est du Pacifique. Les relations phylétiques entre les espèces sont indiquées, mais il n'est pas question de subdiviser le genre *Ampelisca*, vu l'entrelacement des caractères entre les espèces.

## Introduction

Species of the genus *Ampelisca* in the family Ampeliscidae are broadly and abundantly distributed on sand and mud bottoms of continental shelves (Barnard 1969a; Dickinson *et al.* 1980). The majority of about 100 worldwide species are sublittoral forms, but about 20% are bathyal and abyssal. Species in this genus are exclusively marine and spend most of their lives as infaunal tube dwellers feeding on organic detritus (Enequist 1949; Mills 1967a). The breed-

ing behaviour of *Ampelisca* is unknown in most species, but the terminal stage male is known to be pelagic in shallow water species, and mature females are thought to swim to the surface when they are ready to mate (Mills 1967a). It seems likely that bathyal and abyssal members of the genus deviate from this pattern, but their breeding behaviour is completely unknown. The life cycle in most species of *Ampelisca* is unknown, but studies by Mills (1967a) and Kannevorff (1965)

have demonstrated that the life cycle can be as short as a few months (*Ampelisca abdita*) or as long as 2 years (*Ampelisca macrocephala*). Species of *Ampelisca* can be as small as 4-5 mm (*Ampelisca milleri*, *Ampelisca hancocki*) or as large as 25-35 mm (*Ampelisca macrocephala*, *Ampelisca eschrichti*). Zoogeographically, species of *Ampelisca* have been reported to have very broad distributions both geographically and bathymetrically. However, many of the species which have been previously treated as having geographic or bathymetric variants (i.e., *Ampelisca macrocephala*) may turn out to be series of closely related species when examined more critically.

Previous major studies of *Ampelisca* from the Pacific coast of North America are those of Holmes (1908) and Barnard (1954a, 1960, 1967a, 1971a) from California and Oregon. Barnard (1954a, 1960) found 26 species of *Ampelisca* in his extensive studies of the southern California region, and 8 of these species are known from his limited studies of the Oregon coast (Barnard 1971a). Only scattered records exist north of Oregon, and only one species of *Ampelisca agassizi* has been previously reported from British Columbia (Mills 1967b). This study on the systematics and distributional ecology of *Ampelisca* in the region between the Bering Sea and Oregon will attempt to fill in this large gap in our knowledge of this important genus. The systematics and distributional ecology of the other two genera of Ampeliscidae (*Byblis* and *Haploops*) represented in the northeast Pacific coastal waters will be treated in a subsequent paper by Dickinson (in prep.)

## Materials

This study was based primarily on collections in the National Museum of Natural Sciences. These collections range from southeast Alaska to Oregon, but concentrate on British Columbia. The primary source of this material was a series of field expeditions conducted by Dr. E.L. Bousfield and colleagues at the National Museum of Natural Sciences. Station data for expeditions to southern Vancouver Island (1955), Queen Charlotte Islands (1957), northern Vancouver Island (1959), southeastern Alaska (1961) and northcentral British Columbia (1964) were published previously (Bousfield 1957; Bousfield 1963; Bousfield and McAllister 1962; and Bousfield 1968). Data for expeditions to Washington

and Oregon (1966), southern Vancouver Island and Burrard Inlet (1970, 1975 and 1978), and southeastern Alaska (1980) are available in manuscript form from the National Museum of Natural Sciences and will be published in the near future.

Other major sources of *Ampelisca* material used in this study were collections donated to the National Museum of Natural Sciences by Dr. Colin Levings of the Pacific Environmental Institute, Dr. Derek Ellis of the University of Victoria, and material borrowed from Dr. A.G. Carey at Oregon State University, Dr. R. Brusca of the Allan Hancock Foundation, Dr. J.L. Barnard of the U.S. National Museum, and Dr. Mary Nerini of the N.O.A.A. lab in Seattle.

Preserved material and prepared slide mounts of specimens are housed in the National Museum of Natural Sciences, and representative specimens are also deposited in the collections of the United States National Museum, Washington, D.C.

During National Museum of Natural Sciences field trips to Vancouver Island and southeastern Alaska in 1977-1980, Dr. E.L. Bousfield (NMNS) and Mr. Ron Long, Photography Section, Biology Department, Simon Fraser University, made a series of colour photographs of living amphipods as a means of recording their natural pigmentation patterns. These colour transparencies are catalogued in the National Museum of Natural Sciences collections and to date include representatives of *A. careyi*, *A. cristata*, *A. lobata*, *A. pugetica*, and *A. unsocalae*. Regrettably, the transparencies are too few to reveal inter- and intraspecific variation in colour pigmentation for Northeast Pacific *Ampelisca*; the inclusion of colour differences in the species diagnoses would therefore be premature. However, a few brief notes on colour pattern are included for photographed species in the hope that future workers will be stimulated to pursue the investigation of these patterns in *Ampelisca* and other coastal amphipod groups.

## SYSTEMATIC SECTION

### *Ampeliscidae* Bate 1857

*Diagnosis:* Body smooth, pleonites 1-3 smooth or occasionally weakly carinate, urosomite 1 usually carinate, often strongly, especially in male. Urosomites 2-3 fused. Head usually longer than deep, lacking rostrum. Eyes 0-6, (when present)

dorsofrontal pair always with lenses, ventro-frontal pair sometimes with lenses, and dorso-caudal pair always lacking lenses. Antenna 1 usually short, lacking accessory flagellum. Antenna 2 usually long, peduncular segments 4 and 5 elongated. In terminal male stage, brush setae present on ventral surface of peduncular segments 1-2 and basal flagellar segments of antenna 1 and on dorsal surface of peduncular segments 3-5 of antenna 2. Mouthparts slightly modified. Upper lip with median apical notch. Lower lip broad, inner lobe well developed, mandibular lobes weak or lacking. Mandibular molar and palp well developed, left lacinia with 4-5 cusps. Maxilla 1 inner plate weakly setose, outer plate with 11 apical spine teeth. Maxilla 2, inner plate moderately setose. Maxilliped plates well developed, palp strong and dactylate. Anterior coxae usually longer than broad. Coxa 4 strongly excavate posteriorly. Coxae 5-6 anteriorly lobate. Coxa 7 posteriorly lobate. Gnathopod 1 simple or weakly subchelate occasionally sexually dimorphic. Gnathopod 2 elongate, and usually simple. Peraeopods 3 and 4 glandular, segment 5 short, dactyls elongate, simple, with ducts. Peraeopods 5-7, bases broad. Peraeopods 5 and 6, similar in form and size, segment 5 usually with comb teeth on posterior margin, dactyls short. Peraeopod 7 short, different in form than peraeopods 5 and 6. Coxal gills on peraeopods 2-6, usually pleated, sexually dimorphic, mature females having flatter, narrower, and less pleated gills than mature males. Brood plates linear, marginal setae simple. Pleopods strong; retinacula paired, short stemmed, curved tip, one margin toothed. Uropods 1-2, rami usually subequal and narrowly lanceolate. Uropod 3 varies in form, but rami usually long, broadly lanceolate, and setose, outer ramus one-

segmented. Telson bilobate, sometimes sexually dimorphic in size and form, lobes usually deeply and narrowly separated, apices often notched and spinose.

*Ampelisca* Kroyer 1842

*Diagnosis:* Head longer than deep, narrowing anteriorly with anteroventral corner unproduced. Eyes (when present) have lenses in both dorso-frontal and ventrofrontal pairs. Antenna 2, flagellum with more than 5 flagellar segments. Mandibular palp, segment 3 usually much shorter than segment 2. Maxilliped, inner plate short and broad. Anterior coxae much longer than broad. Peraeopods 3-4, segment 5 very short and often partially overhung by segment 4. Peraeopods 5-6, dactyls very short and hook-like. Basal lobe of peraeopod 7 expanded distally, posterior margin oblique, and lacking setae on anterior margin near junction with segment 3. Peraeopod 7 with seven distinct segments, dactyl broad at base. Telson lobes elongated and fused only basally in both sexes.

*Remarks:* The diagnosis of the family Ampeliscidae closely parallels Bousfield's (1978) diagnosis of the superfamily Ampeliscoidea, but encompasses more precisely the generic variability within the family. The diagnosis of the genus *Ampelisca* attempts to strike a middle ground between the narrow diagnosis of Barnard (1969a) and the broad diagnosis of Bousfield (1973). The chief problem in any definition involving the family Ampeliscidae is the poor state of knowledge regarding the monotypic genus *Triodos* K.H. Barnard 1916. Barnard's original description and illustrations are very incomplete, and subsequent work by Griffiths (1976) adds little new taxonomic information.

Key to *Ampelisca* of the Northeast Pacific Region

- 1. Pleon sideplate 3 with an acute tooth on lower posterior corner ..... 2
- Pleon sideplate 3 without an acute tooth on lower posterior corner ..... 9
- 2. Segment 5 of peraeopod 7 with notch in anterior margin and uropod 1 not reaching beyond mid portion of rami of uropod 2 ..... 3
- Segment 5 of peraeopod 7 without notch in anterior margin and uropod 1 reaching end of uropod 2 ..... 4
- 3. Dorsal carina of urosomite 1 saddle shaped; posterior lobe of segment 4 of peraeopod 7 broad, extending ¾ length of segment 5; dorsal surface of telson with long spines ..... *Ampelisca pugetica* p. 17
- Dorsal carina of urosomite 1 not saddle shaped; posterior lobe of segment 4 of peraeopod 7 slender, extending less than ½ length of segment 5; dorsal surface of telson with short spines ..... *Ampelisca eschrichti* p. 18

4.	Uropod 2 lacking subapical spine on outer ramus; posterior margin of pleon sideplate 3 nearly straight; dactyl of peraeopod 7 short and thick .....	<i>Ampelisca hancocki</i>	p. 14
	Uropod 2 with long subapical spine on outer ramus; posterior margin of pleon sideplate 3 convex; dactyl of peraeopod 7 long and slender .....		5
5.	Lower front margin of head concave and parallel to upper margin; pleon sideplate 2 with a tooth on lower posterior corner .....		6
	Lower front margin of head convex or slightly concave but never parallel to upper margin; pleon sideplate 2 without a tooth on lower posterior corner .....		7
6.	Pleon sideplate 3 produced into a large process above tooth; telson, apex of each lobe narrow, lacking large notch; urosomal carina massive not lamellar .....	<i>Ampelisca brevisimulata</i>	p. 26
	Pleon sideplate 3 weakly convex, lacking large process above tooth; telson lobe, apex with large notch; urosomal carina lamellar .....	<i>Ampelisca cristata</i>	p. 25
7.	Dorsal surface of telson with short blunt spines concentrated in a central row .....	<i>Ampelisca macrocephala</i>	p. 20
	Dorsal surface of telson with long slender spines scattered randomly over lobes .....		8
8.	Lower front margin of head concave; antenna 1 reaching end of peduncle of antenna 2; tooth on pleon sideplate 3 short and thick .....	<i>Ampelisca careyi</i>	p. 21
	Lower front margin of head convex; antenna 1 not reaching end of peduncle of antenna 2; tooth on pleon sideplate 3 long and slender .....	<i>Ampelisca unsocalae</i>	p. 23
9.	Rami of uropod 3 short and flattened; basal lobe of peraeopod 7 short only reaching end of segment 3; spines lacking on posterior margin of segment 5 of peraeopods 5 and 6 .....		10
	Rami of uropod 3 long and not flattened; basal lobe of peraeopod 7 extending beyond segment 3; spines present on posterior margin of segment 5 of peraeopod 5 and 6 .....		12
10.	Antenna 1 long, extending beyond peduncle of antenna 2; outer ramus of uropod 2 lacking subapical spine .....	<i>Ampelisca hessleri</i>	p. 6
	Antenna 1 short, not extending beyond peduncle of antenna 2; outer ramus of uropod 2 with subapical spine .....		11
11.	Basal lobe of peraeopod 7, lower posterior margin strongly oblique, eyes present .....	<i>Ampelisca birulai</i>	p. 9
	Basal lobe of peraeopod 7, lower posterior margin weakly oblique, eyes absent .....	<i>Ampelisca plumosa</i>	p. 7
12.	Segment 3 of peraeopod 7 longer than segment 4, mandibular palp segment 2 inflated .....	<i>Ampelisca milleri</i>	p. 15
	Segment 3 of peraeopod 7 subequal to segment 4 in length; mandibular palp segment 2 slender not inflated, sublinear .....		13
13.	Urosomite 1 produced dorsally into a well developed carina; uropod 1 with rami much longer than short stout peduncle; antenna 1 not reaching end of peduncle of antenna 2 .....	<i>Ampelisca agassizi</i>	p. 5
	Urosomite 1 not produced into a carina, uropod 1 with rami shorter than peduncle; antenna 1 reaching end of peduncle of antenna 2 .....		14
14.	Segment 5 of peraeopod 7 lacking spine bearing notch on anterior margin; outer ramus of uropod 1 spinulose on inner margin; inner margin of inner ramus of uropod 3 with six spine-bearing serrations .....	<i>Ampelisca lobata</i>	p. 10
	Segment 5 of peraeopod 7 with spine bearing notch on anterior margin; outer ramus of uropod 1 unarmed on inner margin; inner margin of inner ramus of uropod 3 lacking spine-bearing serrations .....		15
15.	Uropod 3, inner ramus distinctly longer than outer ramus, inner margin of inner ramus bearing a series of large teeth .....	<i>Ampelisca schellenbergi</i>	p. 14
	Uropod 3, inner ramus subequal to outer ramus, inner margin of inner ramus microdentate only .....	<i>Ampelisca fageri</i>	p. 12

*Ampelisca agassizi* (Judd) 1896

Figure 1.

*Byblis agassizi* Judd 1896, pp. 599-603, figs. 9-11

*Ampelisca compressa* Holmes 1903, p. 273;

1905, pp. 408-481, fig. (no number).

*Ampelisca agassizi* Holmes 1905, pp. 418-482, fig. (no number).

:Mills 1967b, pp. 643-645, fig. 3.

:Bousfield 1973, p. 135, pl. 38.

*Ampelisca vera* Barnard 1954a, pp. 23-26, pls. 14-16.

**Material examined:** British Columbia — Queen Charlotte Islands: Bousfield stns. 1957, H1 (6 spec.). J.W. Scoggan stns., 1965, JWS 89, 104, 105, 106 (30 spec.). North central coast: Bousfield stns. 1964, H8, H34, H36, H37, H48, H49 (about 60 spec.). C. Levings, Swanson Bay stns., 1975, 51B-001, 51B-002, 51B-003, 51B-004, 51B-005,

51B-007, 51B-008, 51B-009, 51B-010, 51B-011, 51B-012, 51B-013 (about 400 spec.). Vancouver Island, Shoal Bay, Victoria: J.F.L. Hart, 1949 (2 spec.); Bousfield stns. 1959, 06, V22 (4 spec.). Bousfield stns. 1975, P29b (1 spec.). Bousfield stns. 1976, B-26 (4 spec.). Bousfield stns. 1977, B8 (1 spec.). Verdier Pt., Saanich Inlet, K. Conlan, 1976-77 (about 250 spec.), D.V. Ellis, 1980, Sidney (20 spec.). Southern mainland, Bousfield stns. 1959, N23b. Washington: Bousfield stns. 1955, M10, Bousfield stns. 1966, W13 (2 spec.). Oregon: OSUBI 01280. 46°6'N, 124°8'W, 70 m, 4 Dec. 1974 (1 spec.) OSUBI 01267. 44°26'3N, 124°14.7'W, 60 m, 21 June 1976 (2 spec.)

**Distributional ecology:** Geographic range: North Atlantic, Nova Scotia to Caribbean (Barnard 1954b; Mills 1967b, 1971). North Pacific, Queen Charlotte Islands to Ecuador (Barnard 1954a,

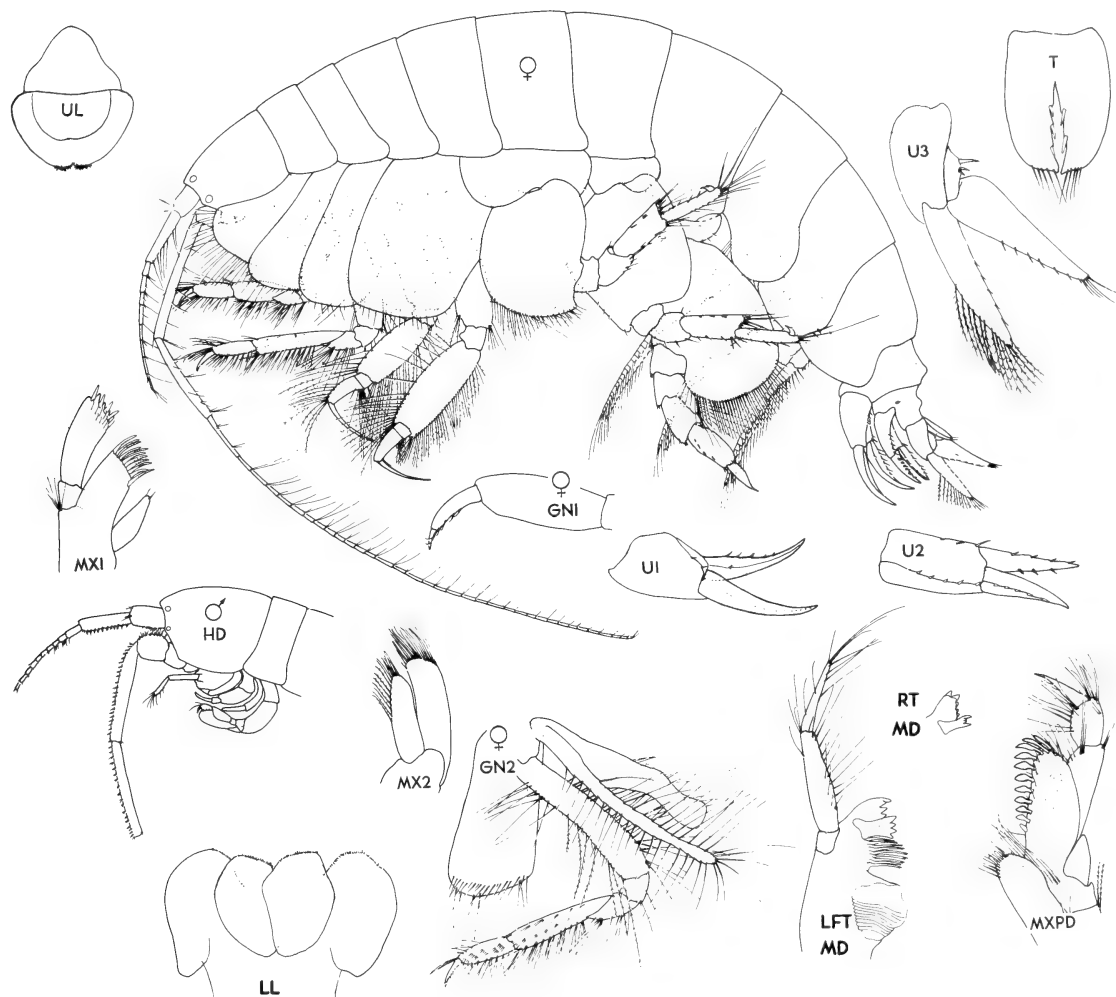


Figure 1. *Ampelisca agassizi* (Judd). Swanson Bay, B.C., ♀ 9 mm ov. Shoal Bay, B.C., ♂ 10 mm

1971a). Bathymetric range: North Atlantic, 5-450 m (Mills 1971; Dickinson *et al.* 1980). North Pacific 0-266 m (Barnard 1971a). NMNS coll. 0-300 m, primarily 40-100 m. Abundance: North Atlantic, up to 15,000/m<sup>2</sup> (Dickinson *et al.* 1980). North Pacific, rarely over 500/m<sup>2</sup>.

*Life cycle:* Ovigerous females found in B.C. waters during July (1), November (1). Terminal males: April (2).

*Diagnosis:* (Female). A medium sized *Ampelisca* (8-11 mm) characterized by: head short, lower front margin oblique nearly straight. Antenna 1 short, not reaching end of peduncle of antenna 2, peduncular segment 2 twice length of segment 1 and with 8-10 long setae on ventral surface, flagellum setae long. Antenna 2, about as long as body, flagellum setae long. Mandibular palp, segment 3 over  $\frac{1}{4}$  length of segment 2. Coxae 1-3 without slit or tooth on lower posterior corner. Gnathopod 1, nearly simple. Gnathopod 2, segment 5 less than twice the length of segment 6. Peraeopod 3, plumose setae along entire posterior margin of segment 4. Peraeopods 5-6, 2-3 rows of weakly developed comb spines along posterior margin of segment 5. Peraeopod 7, basis broad, segment 3 subequal to 4 in length, segment 4 produced posteriorly into a slender, setose lobe extending most of the length of segment 5, segment 6 longer than 5, segment 7 slender and subequal to 5 in length. Uropod 1, peduncle short and deep, rami long reaching end of uropod 2, inner ramus spinulose, outer ramus unarmed. Uropod 2, rami shorter than peduncle, inner ramus spinulose on both margins, outer ramus spinulose on outer margin only. Uropod 3, rami lanceolate, outer ramus bearing more plumose setae than inner. Telson lobes, broad, apices blunt and armed with 4-5 setules, dorsal surface bearing 2-3 pairs of spines along cleft. Pleon sideplate 3, lower posterior corner rounded. Urosomite 1, well developed dorsal carina which is rounded posteriorly. Urosome compressed in length. Gill flattened in mature females, dendritic folds short, narrow and curved downward.

(Male). Very rare in collections. Differ from female in: presence of brush setae on peduncles of antenna 1-2; gills less flattened and dendritic for entire length; urosomite 1, deep notch cut in anterior dorsal surface, massive hood-like carina projecting dorsally over urosomite 2; uropod bearing plumose setae on both margins of both rami.

*Remarks:* Barnard (1960), Mills (1967b) and

the author have compared specimens from the Atlantic and Pacific coasts of North America, and have been unable to find a morphological basis for separating the populations on either side of the Isthmus of Panama. This suggests that evolution in this species must be relatively slow since these populations have been disjunct for at least one million years. *Ampelisca agassizi* is relatively distinct morphologically from other species of the northeast Pacific region (see phenogram Fig. 21) and is easily identified by its combination of rounded pleon side plates, blunt telson, lanceolate uropod 3, and compressed urosome (see Key p. 3).

*Ampelisca hessleri* n. sp.

Figure 2.

*Material examined:* British Columbia — Queen Charlotte Islands: J.W. Scoggan coll. 1965; JWS103 (54°37'N, 133°55'W), 225 m (3 specimens), JWS 104 (54°32'N, 133°25'W), 325 m (1 specimen). North central coast: C. Levings 1963 coll; Swanson Bay (53°0.25'N, 128°30.9'W), 152 m, 4 April 1973; ♀ (6.0 mm) holotype (NMC-C.1981-378), 2 ♀♀ paratypes (NMC-C.1981-377).

*Distributional ecology:* Known only from northern B.C. waters at upper bathyal depths (150-325 m).

*Diagnosis:* (Female). A small *Ampelisca* (6-8.0 mm) characterized by: head, eyes present, lower front margin oblique and convex. Antenna 1 long, extending well beyond peduncle of antenna 2, peduncular segment 2 only slightly longer than 1, flagellum setae of medium length. Antenna 2 about  $\frac{3}{4}$  body length, peduncular segment 4 about twice length of antenna 1 peduncular segment 2, flagellum setae of medium length. Mandibular palp, segment 3 about half length of segment 2. Coxae 1-3, lower posterior corner toothed. Gnathopod 1, palm elongate extending  $\frac{2}{3}$  posterior margin of segment 6. Gnathopod 2, segment 5 less than twice the length of segment 6. Peraeopod 3, plumose setae confined to distal third of posterior margin of segment 4. Peraeopods 5-6, posterior margin of segment 5 unarmed. Peraeopod 7, basal lobe relatively slender and lower posterior margin obliquely rounded, segment 3 subequal to 4 in length, segment 4 with posterior lobe weak and sparsely setose, segments 5 and 6 subequal in length, segments 3-7 slender and stick-like. Uropod 1, peduncle stout, rami shorter than



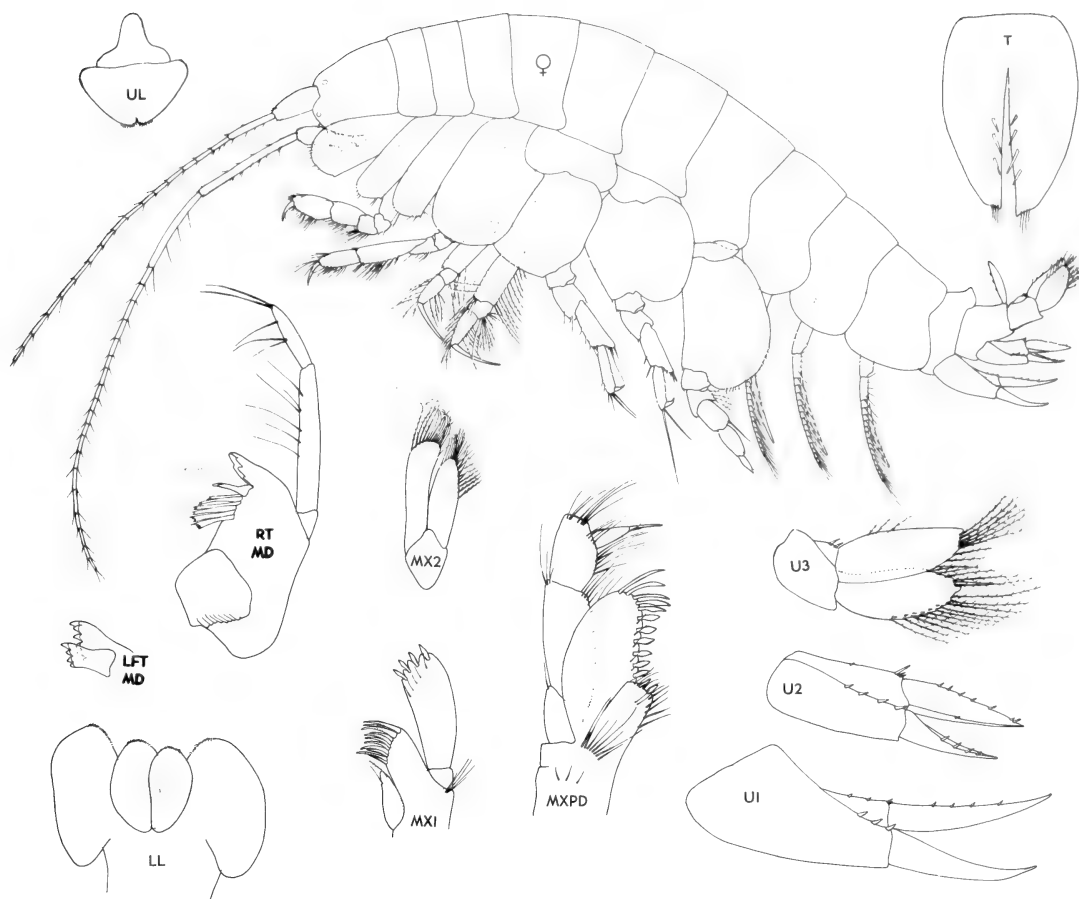


Figure 2. *Ampelisca hessleri* n.sp. Swanson Bay, B.C., ♀ holotype, 6 mm

peduncle, inner margin of inner ramus with 4 spines, outer ramus unarmed. Uropod 2, peduncle longer than rami, outer ramus shorter than inner, both rami spinulose, no apical spine on outer ramus. Uropod 3, rami flattened, broad and foliaceous, distal margins of outer ramus serrated with a plumose seta set in each serration, apex of inner ramus notched medially with 6-8 plumose setae set in notch. Telson lobes, tapering to a blunt tip bearing 3-4 setules, dorsal surface with 3-4 short spines along each side of the cleft. Pleon side plate 3 rounded, without tooth at lower posterior corner. Urosomite 1 elevated into carina which is upturned posteriorly. Gills flattened and unpleated in mature females.

(Male). Unknown.

**Remarks:** This new species is very similar to *A. plumosa* Holmes and *A. birulai* (see phenogram Fig. 21), but these species can be distinguished by the relative lengths of antennae, shape

of the basal lobe of pereopod 7, stoutness of rami of uropod 3, and the presence or absence of a tip spine on uropod 2 (see key p. 3 and Figs. 2-4).

**Etymology:** This species is named in honour of Dr. Robert Hessler who has contributed greatly to our knowledge of deep sea benthic ecology, and who also has a special interest in the evolution of peracarid crustaceans.

#### *Ampelisca plumosa* Holmes 1908

Figure 3.

*Ampelisca plumosa* Holmes 1908, pp. 509-510, figs. 18.

:Barnard 1960, pp. 30-31, fig. 8

**Material examined:** Southern California — North Coronado Island: Off San Diego, 1130-1190 m, USNM cat. no. 38542, holotype (13.0 mm) sub. ♂.

**Distributional ecology:** Known only from

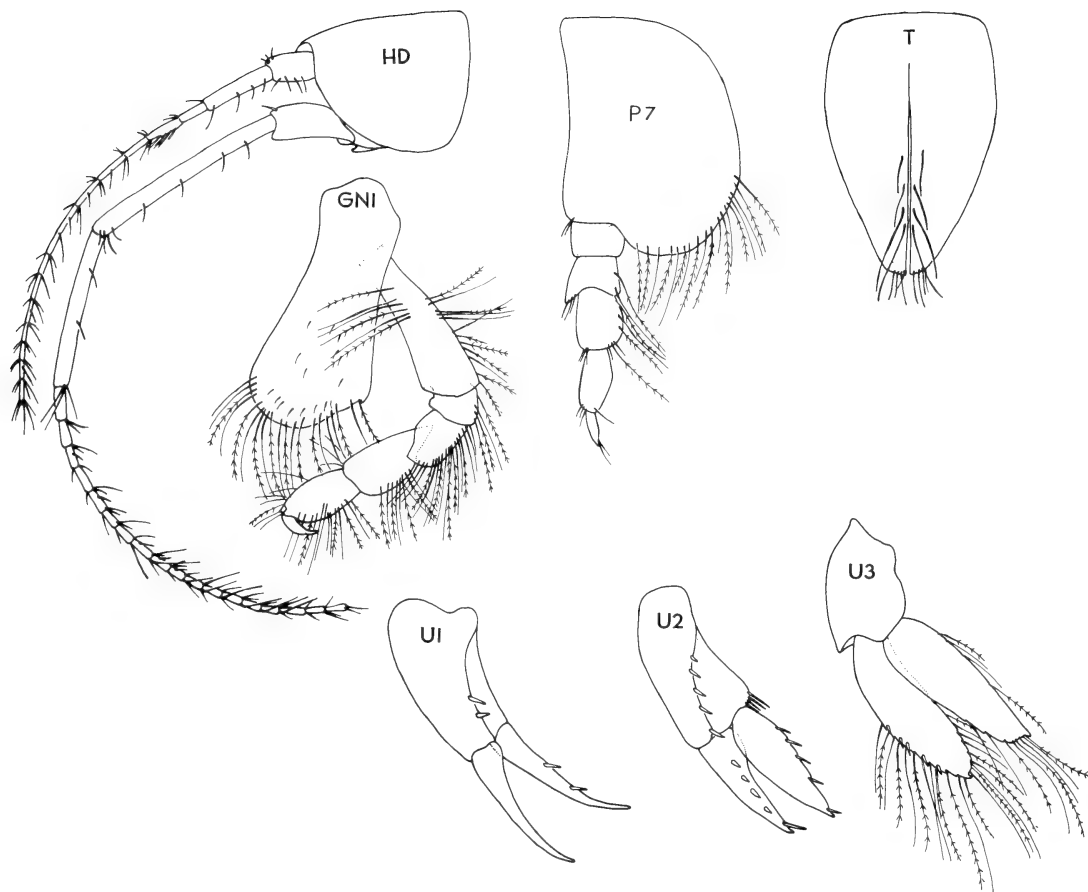


Figure 3. *Ampelisca plumosa* Holmes. North Coronado Island, California. ♂ holotype, 13 mm, subadult

bathyal depths off southern California (Holmes 1908, Barnard 1960). Dickinson and Carey's (1978) records in abyssal depths off Oregon are another new species in this group.

**Diagnosis:** The diagnosis of this species is based solely on a subadult male (holotype 13.0 mm) which usually differs from the female only in the structure of the gills and the presence of penal papillae. This species is characterized by: head, eyes absent, lower front margin of head nearly vertical. Antenna 1 just reaching end of peduncle of antenna 2, peduncular segment 2 about one and half times length of segment 1, flagellum setae medium length. Antenna 2 about body length, peduncular segment 4 long, more than twice length of antenna 1 peduncular segment 2, flagellum setae medium length. Coxae 1-3, lower posterior corner toothed. Gnathopod 1, palm short, extending only  $\frac{1}{3}$  length of posterior margin of segment 6. Gnathopod 2, segment 5 elongate, more than twice length of segment 6. Peraeopod 3, plumose setae along

entire posterior margin of segment 4. Peraeopods 5-6, posterior margin of segment 5 unarmed. Peraeopod 7, basal lobe relatively broad and lower posterior margin gently rounded, segment 3 subequal to 4 in length, segment 4, posterior lobe weakly developed and sparsely setose, segments 5 and 6 subequal in length, segments 3-7 slender, stick-like. Uropod 1, peduncle stout, rami slightly shorter than peduncle, inner margin of inner ramus with 2 spines, outer ramus unarmed. Uropod 2, peduncle longer than rami, outer ramus smaller than inner ramus bearing a medium length apical spine, both rami spinulose. Uropod 3, rami flattened, relatively slender, and foliaceous; distal margins of outer ramus serrated with a plumose seta set in each serration, apex of inner ramus notched medially with 6-8 plumose setae set in notch. Telson lobes tapering to a blunt tip bearing 3-4 setules, dorsal surface with 4 pairs of long spines along cleft. Pleon sideplate 3, posterior corner rounded, without a tooth. Urosomite 1 elevated into a carina which

is upturned posteriorly. Gills highly pleated in subadult male.

(Pelagic terminal male). Unknown.

**Remarks:** This species is unknown from study area, but it is included to help distinguish it from *A. hessleri* n.sp. and *A. birulai* Brügger. It was also thought a more critical diagnosis and more detailed illustrations would be useful to future workers since representatives of this species group of *Ampelisca* seem to be common at bathyal and abyssal depths of the northeast Pacific.

***Ampelisca birulai* Brügger 1909**

Figure 4.

*Ampelisca birulai* Gurjanova 1951, p. 310, fig. 173.

:Shoemaker 1955, p. 10, fig. 2,n-q, 3,a-c

**Material examined:** Alaska — Beaufort Sea (71°21.9N,152°33.4W), 99 m, 3 November 1976, O.S.U.B.I. 00985 (1 ov. ♀); Bering Sea: St.

Lawrence Island (64°N,169°W), July 1980, J. Oliver coll., (3 specimens).

**Distributional ecology:** Geographic range: Arctic Ocean and Bering Sea (Shoemaker 1955). Bathymetric range: 10-100 m (Shoemaker 1955).

**Life cycle:** Ovigerous females found in Beaufort Sea during November (1).

**Diagnosis:** A medium sized *Ampelisca* (8-10 mm) characterized by: head, eyes present, lower front margin oblique, nearly straight. Antenna 1 reaching just beyond peduncle of antenna 2, peduncular segment 2 subequal to segment 1, flagellum setae medium length. Antenna 2 about half body length, peduncular segment 4 more than twice length of antenna 1, peduncular segment 2, flagellum setae medium length. Mandibular palp, segment 3 about  $\frac{2}{3}$  length of segment 2. Coxae 1-3, lower posterior corner strongly toothed. Gnathopod 1, segments 5 and 6 stout, palm short and deep, almost vertical,

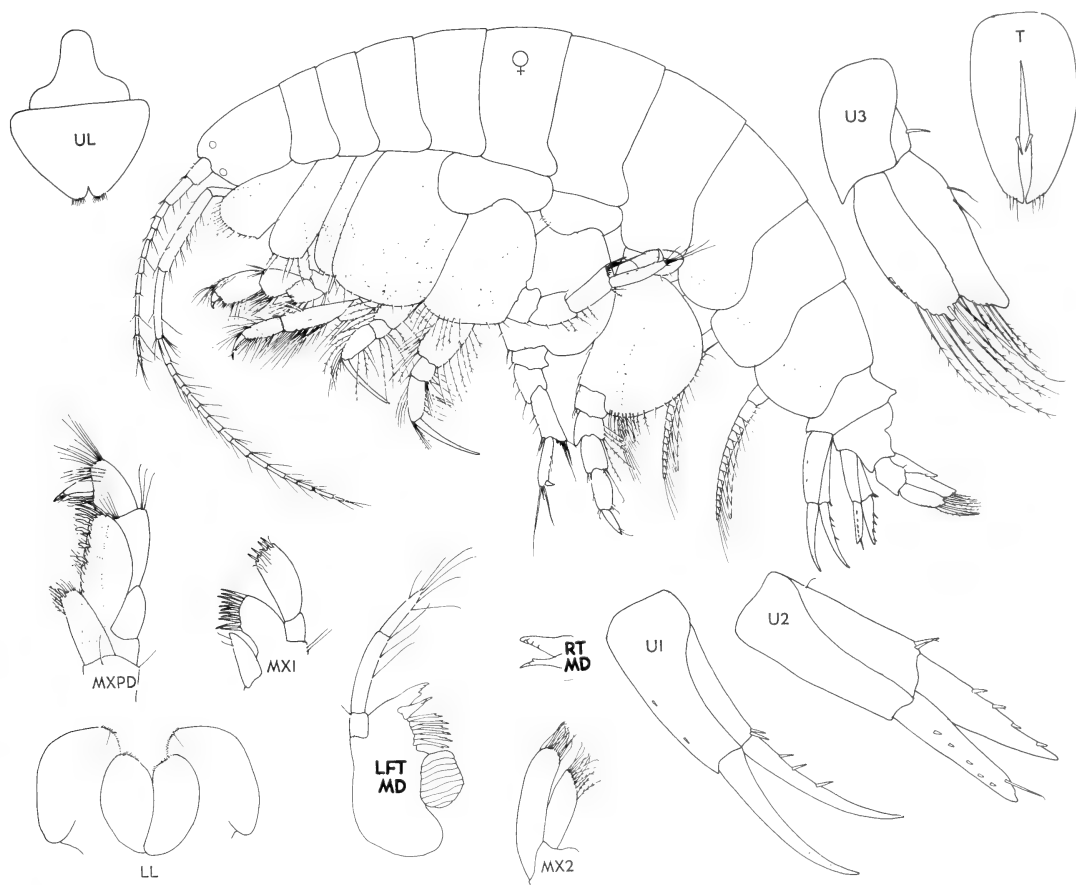


Figure 4. *Ampelisca birulai* Brügger. Pitt Point, Beaufort Sea, Alaska. ♀ 8 mm, ov.

dactyl short and thick. Gnathopod 2, segment 5 less than twice length of segment 6. Peraeopod 3, plumose setae sparsely distributed along entire posterior margin of segment 4. Peraeopods 5-6, posterior margin of segment 5 unarmed. Peraeopod 7, basal lobe relatively broad with lower posterior margin steeply oblique, segment 3 subequal to 4 in length, segment 4 posterior lobe weak and sparsely setose, segments 5 and 6 subequal in length, segments 3-7 slender and stick-like. Uropod 1, rami and peduncle subequal in length, inner margin of inner ramus armed with 3 spines, outer ramus unarmed. Uropod 2, peduncle longer than rami, outer ramus shorter than inner and bearing a sub-apical spine, both rami spinulose. Uropod 3, rami flattened, relatively slender, and foliaceous; distal margins of outer ramus serrated with plumose seta set in each serration, apex of inner ramus notched

medially with 4-6 plumose setae set in notch. Telson lobes each tapering to a blunt tip bearing 3-4 setules, dorsal surface with 1-2 pairs of short spines along cleft. Pleon sideplate 3, lower posterior corner rounded without a tooth. Urosomite 1, elevated into a carina which is upturned posteriorly. Gills flattened and unpleated in mature female.

(Pelagic terminal male). Unknown.

*Remarks:* *Ampelisca birulai* is extremely similar to *A. plumosa* (see phenogram fig. 21), but is easily distinguished by the shape of its basal lobe on peraeopod 7 (see key p. 3).

***Ampelisca lobata* Holmes 1908**

Figure 5.

*Ampelisca lobata* Holmes 1908, pp. 517-518, fig. 25

:Barnard 1954a, pp. 11-14, pls. 5-6

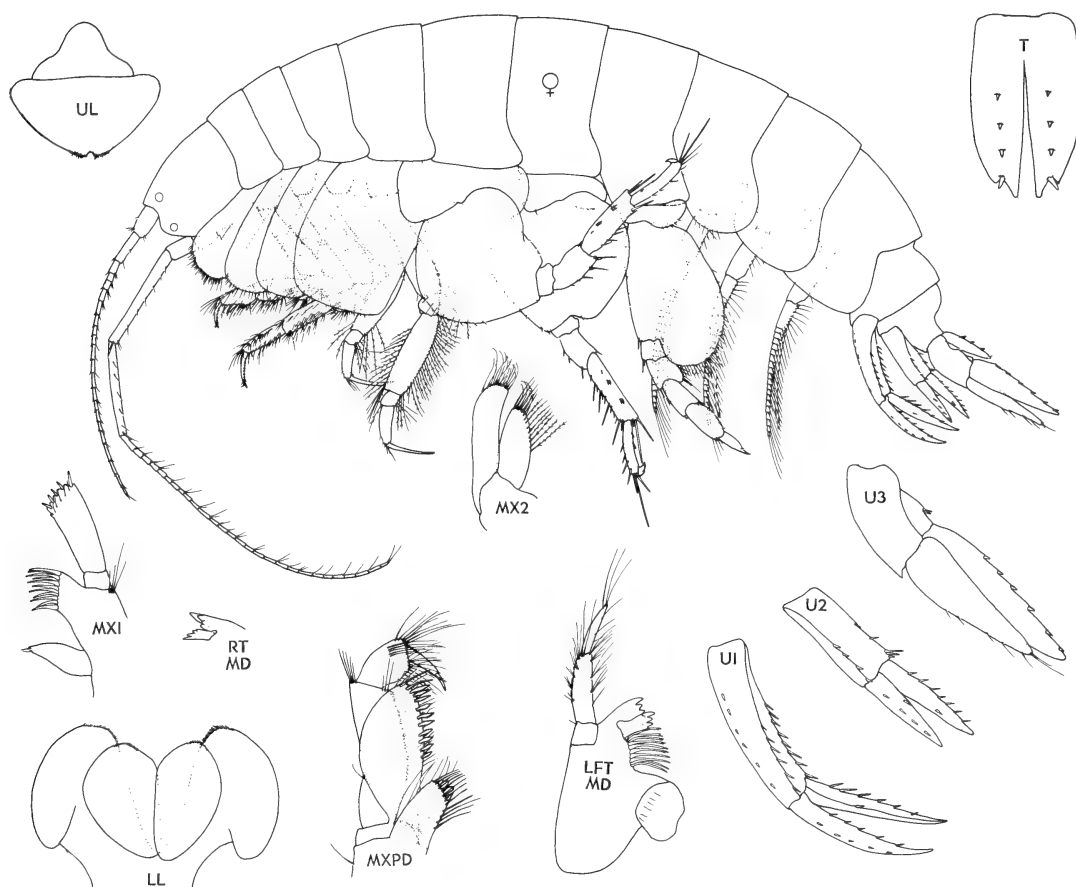


Figure 5. *Ampelisca lobata* Holmes. Stn. H21 (1964), North Bank Island, B.C. ♀ 7 mm, ov.

*Ampelisca articulata* Stout 1913, pp. 639-640

**Material examined:** British Columbia — Queen Charlotte Islands: Bousfield stns. 1957; H2a, H14, W9, W12 (4 specimens). J.W. Scoggan stns., 1965; JWS 106 (4 specimens). Northcentral coast: Bousfield stns., 1964; H10, H21, H26, H28, H31, H34, H36, H50 (11 specimens). L. Marhue stns., 1966; LM17 (1 specimen). Vancouver Island: NMNS coll. 1909; Ucluelet (5 specimens), NMNS coll. 1931; Nanoose Bay, Nanaimo (1 specimen). Bousfield stns., 1955; F1 (3 specimens). Bousfield stns., 1959; V4b, V6, 01, 03, 05, 07b (50 spec.). N.A. Powell, NMNS coll. 1969; Wiffen Spit (2 specimens). Bousfield stns., 1970; P702, P713, P719 (3 specimens). Bousfield stns., 1975; P5b, P5c, P17e (30 specimens). Bousfield stns., 1976; B26, B27 (100 specimens). USNM coll. Round Island, Nanoose Bay, Ucluelet (6 specimens). D.V. Ellis, Sidney Harbour stns., 1979; 1601, 2401, 2602, 3401 (4 specimens). Southern mainland coast: Bousfield stns., 1977; E3, P3, (32 specimens).

**Distributional ecology:** Geographic range — Queen Charlotte Islands to Baja California (Barnard 1954a,b, 1967a, 1971a). Records from Caribbean Sea (Barnard 1954b) and South America (Barnard 1954a) were unillustrated and are suspect until examined by more recent critical standards. Bathymetric range: 0-183 m with southern submergence (Barnard 1969b). 0-144 m off British Columbia but most commonly 0-40 m. Sediment preference: Strong association with plants (Barnard 1969b). Mixed bottoms of rock and sand off British Columbia.

**Life cycle:** Ovigerous females found in B.C. waters during May (1), July (7), August (1), November (1).

**Diagnosis:** (Female). A medium sized *Ampelisca* (7-9 mm) characterized by: head, lower front margin oblique and convex. Antenna 1 extending just beyond end of peduncle of antenna 2, peduncular segments 1 and 2 subequal, flagellum with short setae. Antenna 2 about two thirds body length, flagellum with medium length setae. Mandibular palp segment 3 about four-fifths length of palp segment 2. Gnathopod 1, palm elongate. Gnathopod 2, segment 5 less than twice length of segment 6. Coxae 1-3 slender, slit at lower posterior corner. Peraeopod 3 slender, segment 4 bearing plumose setae only on distal third of the posterior margin. Peraeopods 5 and 6, three sets of comb spines on posterior margin of segment 5. Peraeopod 7, basal lobe deep and

relatively slender, segment 4 longer than 3, with a small setose posterior lobe, segments 5 and 6 subequal in length. Uropod 1 reaching to end of uropod 2, both rami spinulose. Uropod 2, outer ramus slightly shorter than inner ramus, both margins of both rami spinulose. Uropod 3, inner ramus longer than outer ramus, inner ramus strongly serrate along inner margin, with six blunt spines each set in a serration, inner ramus without setae, outer ramus with a few terminal setae. Telson, lobes notched laterally at tip, each notch bearing a short blunt spine, dorsal surface of each lobe with 3-5 short blunt spines in a central row. Pleon sideplate 3 usually quadrate at lower posterior corner, occasionally minutely toothed in large specimens. Urosomite 1 raised only slightly dorsally, posterior edge flush with urosomite 2. Gills flattened, with dendritic folds short, narrow and curved downward.

(Male). None in NMNS collections. According to Barnard (1954a), mature males differ in having: brush setae on peduncles of antenna 1 and 2, flagellum of both antenna elongated; gnathopod 1, segment 6-narrowed distally (see *A. pugetica* figure); uropod 3, rami subequal in length, inner ramus lacking serrations, both margins of both rami setose. Subadult males have less flattened gills with more dendritic folds. Presumably, adult males would have even more complexly folded gills.

**Remarks:** *Ampelisca lobata* is most similar to *A. fageri* (see discussion and phenogram), especially in structure of urosome, gills, and telson. However, the two species are easily separated on differences in peraeopod 7 and uropod 3 noted in the key.

A single photograph of *A. lobata* (#AAA lab. 1) shows the colour patterns in the female specimen from the Burrard Inlet region. The majority of the body is translucent with faint traces of red pigment on the antennae and peraeopods. The anterior portion of the head is highly pigmented in cardinal red and yellowish white. The red pigment is concentrated around the eyes and is probably the subcuticular non-reticular screening pigment referred to in Halberg *et al.* 1980. The yellowish white pigment is located peripheral to the major concentrations of red pigment. It appears closer to the cuticular surface, and is more granular in appearance. The distal segments of the anterior peraeopods also have scattered spots of white pigment.

*Ampelisca fageri* n. sp.

Figures 6-7.

*Ampelisca schellenbergi* Barnard 1954a in part, pp. 14-16, pls. 7a, c, pls. 8a, b, d, e, f, g.

**Material examined:** British Columbia — Whiffen Spit, Sooke Basin, Vancouver Island; (48°21'N, 123°44'W), Bousfield stns., 1955; F1, gravelly sand among boulders, 31.3‰, 10.9°C, intertidal, 17 August 1955; holotype ♀ 8.0 mm br.II (NMC-C.1981-379); 2 ♀♀ and 6 imm. paratypes (NMC-C.1981-380). Additional records: North-central coast: Bousfield stns., 1964; H1 (3 specimens), Vancouver Island, Bousfield stns., 1955; P6a (1 specimen). Bousfield stns., 1959; V5b (1 specimen). N.A. Powell stns., 1969; Wiffen Spit (#319) (1 specimen). Bousfield stns., 1970; P702, P711 (6 specimens).

Mexico — Gulf of California, San Estaban Island (28°48'N, 112°34'W); A. Hancock Foundation stns., 562, 729 (200 specimens).

**Distributional ecology:** Geographic range — Northeastern Pacific, North central coast of British Columbia (51°39'N, 128°09'W) to the Gulf of California, Mexico. Bathymetric range — intertidal in B.C. showing a submergence to the south but rarely deeper than 40 m (Barnard 1967a). Sediment preference — mixed bottom areas of sand and boulders.

**Life cycle:** Ovigerous females found in B.C. waters during July (1), August (2). Pelagic males, none.

**Diagnosis:** (Female). Medium-sized *Ampelisca* (8 mm) characterized by: head, lower front margin convex. Antenna 1 reaching end of peduncle of antenna 2, peduncular segment 2 slightly larger than 1, flagellum setae short. Antenna 2 about ¾ body length, flagellum setae very long. Mandibular palp, segment 3 subequal to segment 2 in length. Coxae 1-3, slit at lower posterior corner, long setae along entire ventral

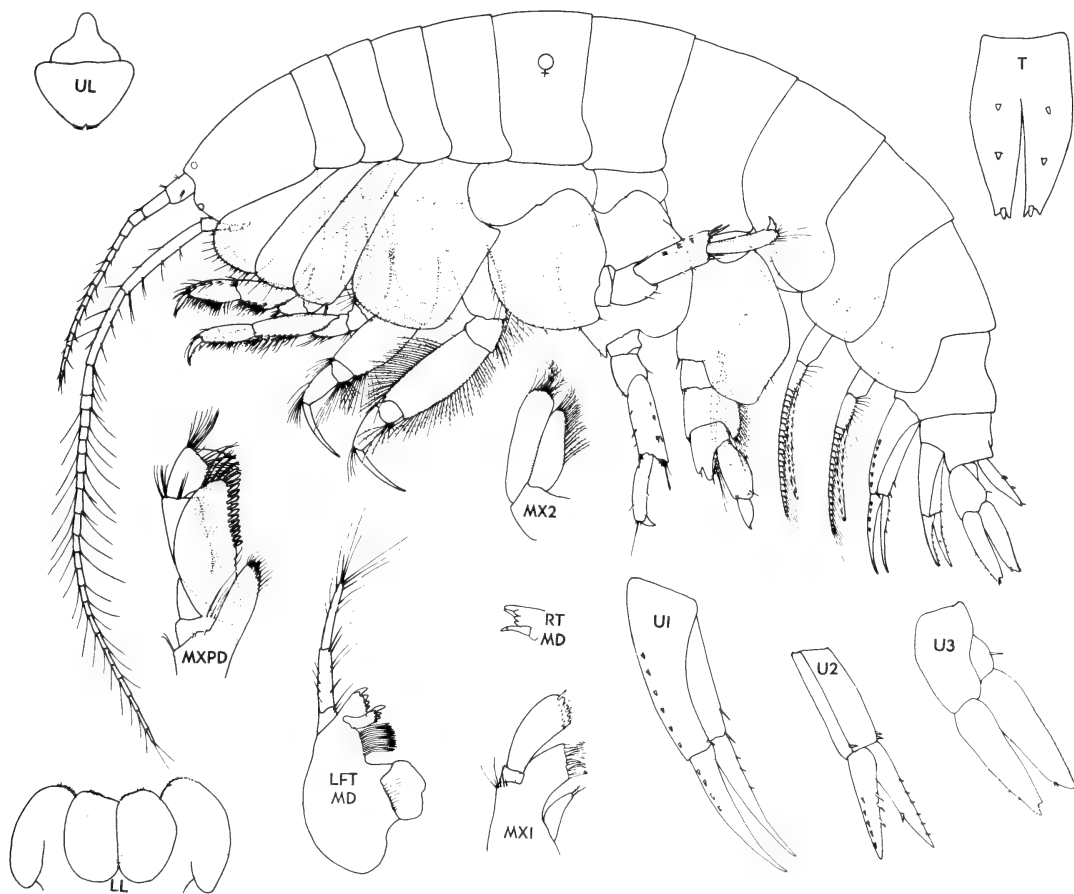


Figure 6. *Ampelisca fageri* n.sp. Wiffen Spit, Vancouver Island, B.C. ♀ holotype, 8 mm, br II

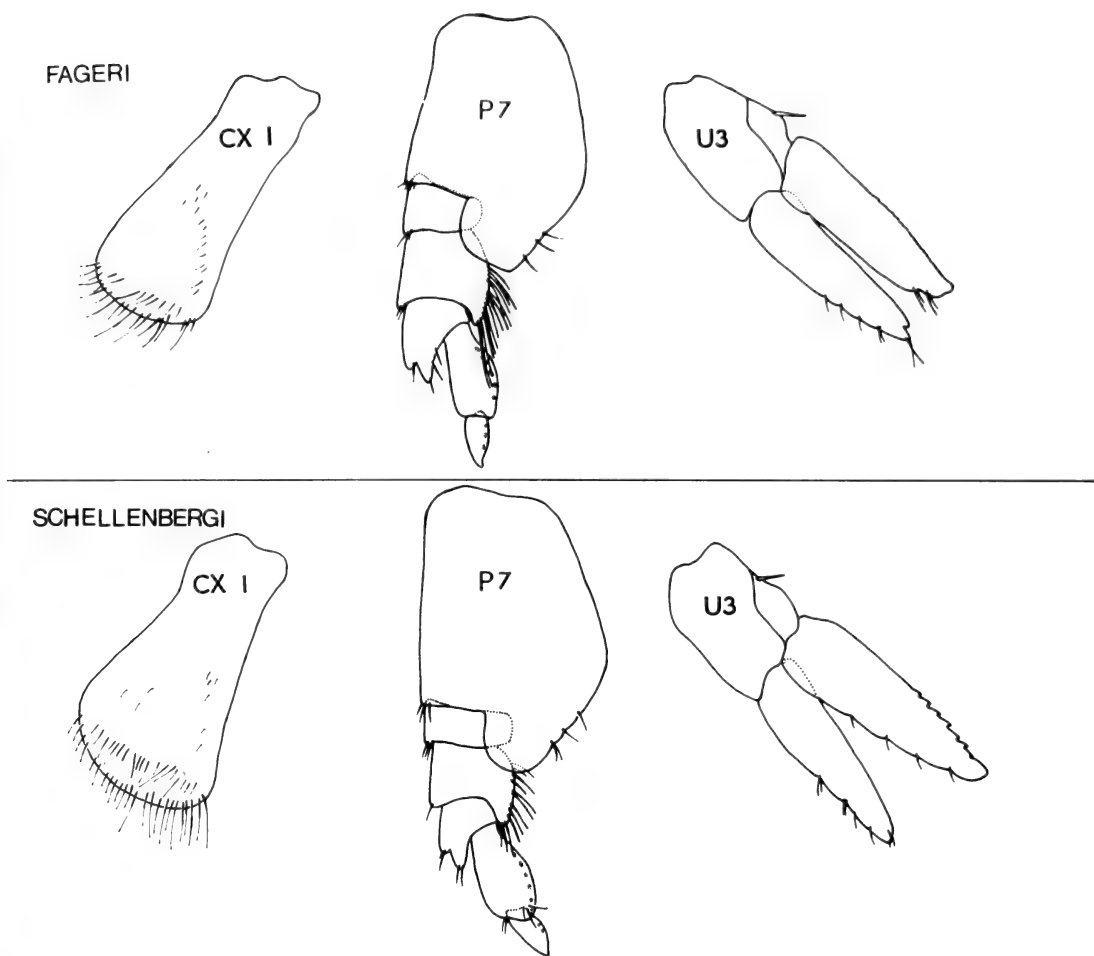


Figure 7. *Ampelisca fageri* n.sp. Wiffen Spit, Vancouver Island, B.C. ♀ holotype, 8 mm, br. II, upper panel. *Ampelisca schellenbergi* Shoemaker. Dog Island, Gulf coast, Florida, ♀ 9 mm, br. II, lower panel.

margin. Coxa 1 weakly expanded distally. Gnathopod 1, palm shallow and elongate. Gnathopod 2, segment 5 short, less than twice as long as segment 6. Peraeopod 3 stout, subequal to peraeopod 4, marginal setae restricted to distal third of segment 4. Peraeopods 5 and 6, bases broad, posterior margin of segment 5 armed with 2-3 sets of comb spines. Peraeopod 7, lower posterior margin of basis oblique nearly straight, cut by a series of unevenly spaced shallow setae bearing notches, segment 4 longer than 3 and very broad, posterior lobe of segment 4 bearing 14-16 plumose setae, anterior

margin of segment 5 twice length of posterior margin and cut by a deep spine bearing notch, segment 6 long and attached near posterior margin of segment 5, segment 7 short and stout. Uropod 1 reaching end of uropod 2, inner margin of inner ramus spinulose, outer ramus with basal spines only. Uropod 2, peduncle longer than rami, both margins of both rami spinulose. Uropod 3 short, inner ramus slightly longer than outer ramus, outer ramus notched at tip, inner edge of inner ramus microdentate only, no large teeth present. Telson, lobes notched apically, a single blunt spine in each notch, dorsal surface of

each lobe with 2 blunt spines in a central row. Pleon side plate 3, lower posterior corner nearly quadrate, lacking tooth. Urosomite 1, dorsal surface weakly produced, posterior margin flush with urosomite 2. Gills in mature females flattened, dendritic folds short, narrow, and curved downward.

(Male). Unknown. Probably similar in form to that described for *A. schellenbergi* in Barnard (1954a).

**Remarks:** This species is very similar to *Ampelisca schellenbergi* Shoemaker 1933, and Barnard (1954a, 1967a, 1969b) treated it as merely a geographic variant. The two forms can be separated on the basis of the shape and setation of coxa 1, the shape of the basal lobe of pereopod 7, and the relative size and shape of the rami of uropod 3 (see Fig. 7). In addition to the morphological differences, the geographic range and differences in ecology confirm that these two forms are different species.

**Etymology:** The species is named in honour of the late Dr. E.W. Fager of the Scripps Institute of Oceanography who was a brilliant and influential teacher of the use of quantitative methods in marine ecology.

***Ampelisca schellenbergi* Shoemaker 1933**

Figure 7.

*Ampelisca schellenbergi* Shoemaker 1933, pp. 3-5, fig. 2.

:Barnard 1954a, in part pp. 14-16, pls. 7b,d,e, 8c.

**Material examined:** Florida — Gulf coast: Dog Island, Franklin County, NMNS coll. 1965 (1 specimen); Tampa Bay, NMNS coll. 1976 (1 specimen).

Costa Rica — Pacific coast: Salinas Bay, A. Hancock Foundation stn. 478 (17 specimens).

**Remarks:** This species is not found north of Central America, and is included only as an aid in defining *A. fageri* n.sp. (see Fig. 21 and discussion p. 30). *Ampelisca schellenbergi* is reported from the Gulf of Mexico, Caribbean Sea, and in the eastern Pacific from Costa Rica to Peru (Barnard 1954a, 1954b). Barnard's (1967a, 1971b) records of this species from Hawaii are suspect, and should be re-examined more critically considering the disjunct nature of the Hawaiian population. However, it should be noted that the Hawaiian form is much closer to *A. schellenbergi* than to *A. fageri* in the form of its uropod 3, coxa 1, and pereopod 7.

***Ampelisca hancocki* J.L. Barnard**

Figure 8.

*Ampelisca hancocki* Barnard 1954a, pp. 37-38, pl. 26.

**Material examined:** British Columbia — North central coast: C. Levings stns., 1972; Ocean Falls (52°20'N, 127°50'W), (1 specimen). Bousfield stns., 1964; H1, H37, H55 (12 specimens). Vancouver Island: Bousfield stns., 1975; P14a, P26 (2 specimens). Bousfield stns., 1976; B26, B27 (10 specimens). Bousfield stns., 1977; B1 (1 specimen). P. O'Rourke stns., 1979; French Creek (49°20'N, 124°20'W), FC1, FC2, FC10, FC11, FC12 (15 specimens). Southern mainland: Bousfield stns., 1977; P2 (1 specimen). Bousfield stns., 1978; V1, (1 specimen).

**Distributional ecology:** Geographic range: British Columbia (52°20'N, 127°50'W) to Costa Rica (Barnard 1971). Bathymetric range: 9-200 m (Barnard 1971). 0-73 m (NMNS coll.). Sediment preference: fine sand.

**Life cycle:** Ovigerous females found in B.C. waters in July (1), August (6). Pelagic males in May (1), July (1), August (1).

**Diagnosis:** (Female). A small *Ampelisca* (4-6 mm), characterized by: head, lower front margin oblique nearly straight. Antenna 1 short not reaching end of peduncle of antenna 2, peduncular segments 1 and 2 subequal in length, flagellum setae medium length. Antenna 2, about body length, flagellum setae medium length. Mandibular palp, segment 3 about  $\frac{3}{4}$  length of segment 2. Coxae 1-3, lower posterior corner toothed. Gnathopod 1, stout, palm shallow and elongate. Gnathopod 2, segment about  $\frac{2}{3}$  length of segment 5. Pereopod 3, plumose setae on distal half of posterior margin of segment 4. Pereopods 5-6, only single spine on posterior margin of segment 5. Pereopod 7, basal lobe broad with lower posterior margin obliquely rounded, segment 3 subequal to 4 in length, segment 4 produced into a tapering setose posterior lobe, segment 6 inflated and only slightly longer than 5, segment 7 very short. Uropod 1, almost reaching end of uropod 2, peduncle and rami subequal in length, outer ramus unarmed. Uropod 2, rami shorter than peduncle, outer margin of outer ramus spinulose, both margins of inner ramus spinulose. Uropod 3, rami slender, lanceolate, and sparsely setose at tips: Telson lobes, broad rounded apices with two setae and a small medial notch bearing a blunt spine, dorsal surface with two pairs of spines along cleft. Pleon



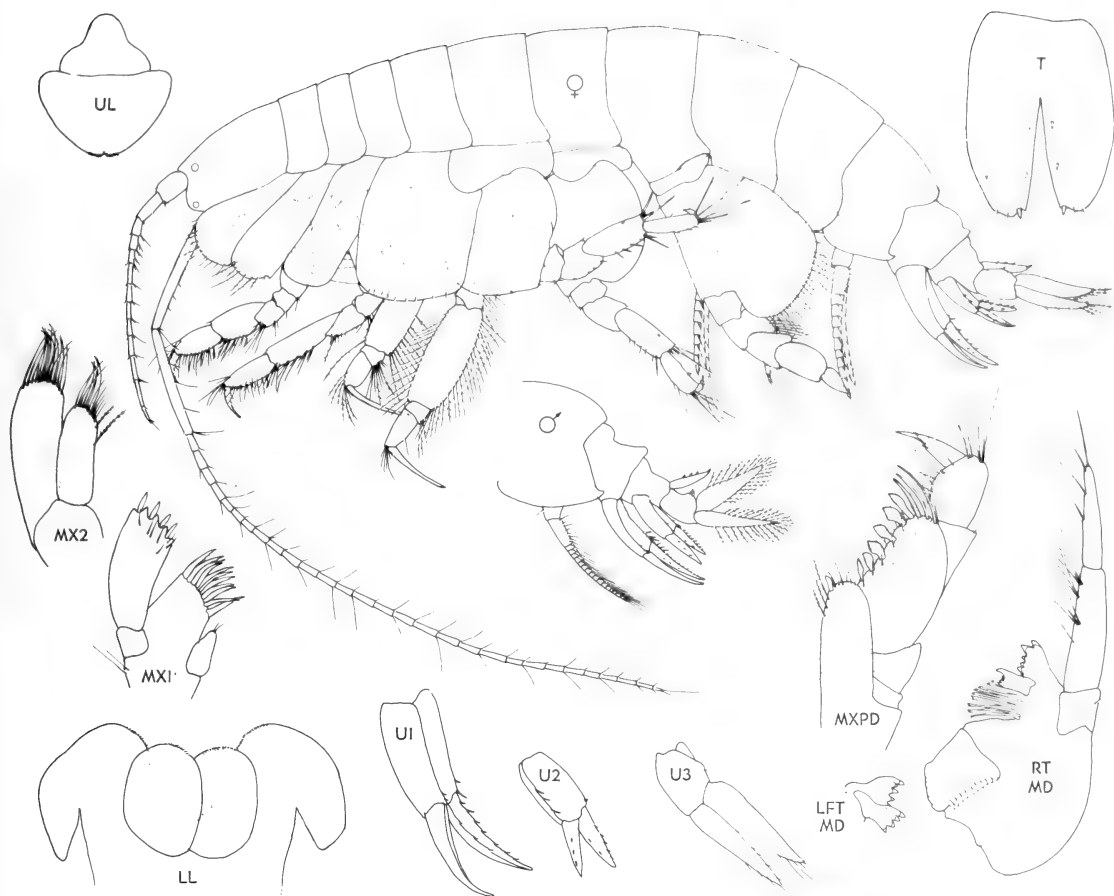


Figure 8. *Ampelisca hancocki* J.L. Barnard. Diana Island, Vancouver Island, B.C. ♀ 5 mm, ov. Departure Bay, Vancouver Island, B.C. ♂ 6 mm.

sideplate 3, posterior margin nearly straight ending in medium sized acute tooth. Urosomite 1, weakly produced dorsally into a saddle shaped carina. Gills flattened, dendritic folds short, narrow, and curved downward.

(Male). Pelagic males (5.0-6.0 mm) differ from females in: presence of brush setae on peduncles of antenna 1 and 2, flagellum of antenna 1 elongate, extending beyond end of peduncle of antenna 2, flagellum setae of both antennae very short. Urosomite 1, dorsal surface notched anteriorly and produced into a hoodlike carina posteriorly. Uropod 3, rami bearing plumose setae on all margins. Gills with long, straight dendritic folds.

**Remarks:** *Ampelisca hancocki* is quite distinct from other Northeast Pacific *Ampelisca* and is easily identified by the straight posterior margin

of pleon sideplate 3, the short dactyl on pereopod 7, and the rounded apices of the telson lobes (see key p. 3). *A. hancocki* is also the only *Ampelisca* in the region which has an acute tooth on pleon sideplate 3 but lacks a subapical spine on uropod 2.

#### *Ampelisca milleri* J.L. Barnard

Figure 9.

*Ampelisca milleri* Barnard 1954a, pp. 9-11, pls. 3-4

**Material examined:** California — Dillon Beach: D. Markowitz coll. 16 April 1979 (30 specimens).

**Distributional ecology:** Geographic range — Dillon Beach, California to Ecuador and the Galapagos Islands (Barnard 1967a). Bathymetric range: 0-187 m (Barnard 1971).

**Life cycle:** Ovigerous females found in Cali-

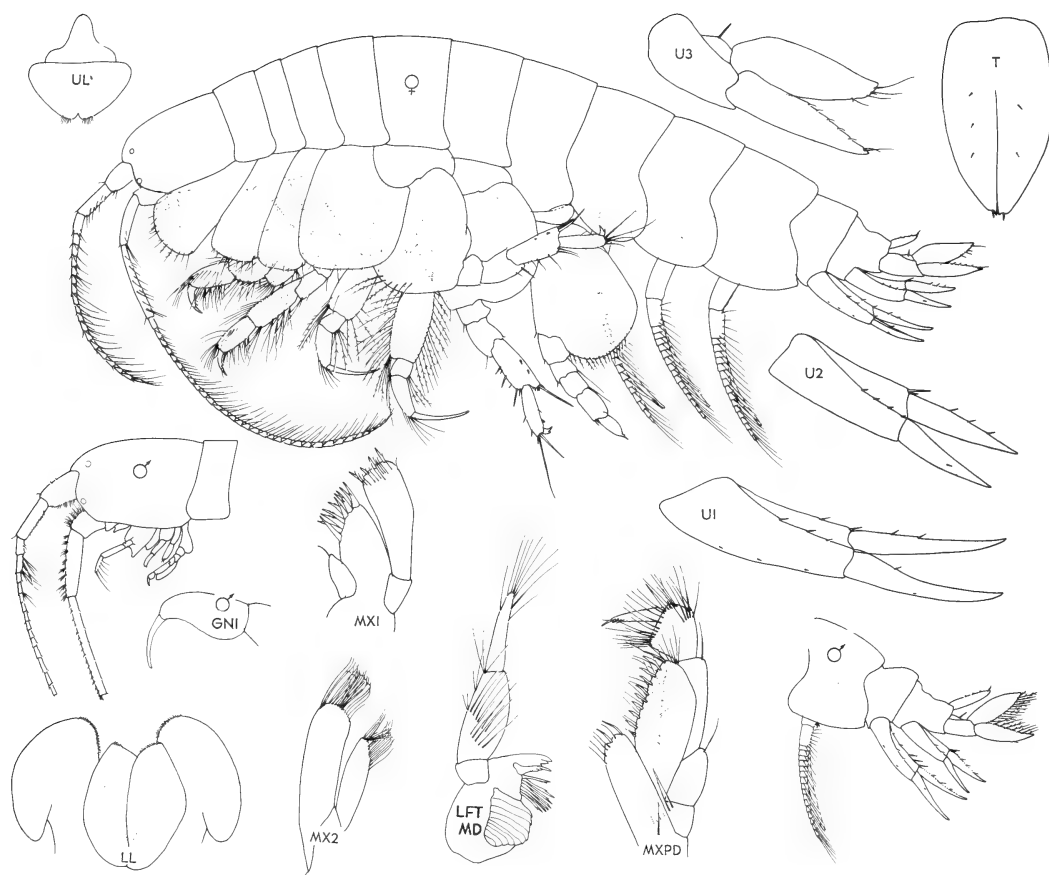


Figure 9. *Ampelisca milleri* J.L. Barnard. Dillon Beach, California. ♀ 6 mm, ov., ♂ 6 mm

fornia waters in April (5). Pelagic males in April (15).

**Diagnosis:** (Female). A small *Ampelisca* (5-6 mm) characterized by: head, lower front margin convex. Antenna 1 reaching well beyond end of peduncle of antenna 2, peduncular segment 2 distinctly longer than segment 1, flagellum setae long. Antenna 2 short, less than  $\frac{2}{3}$  body length, flagellum setae long. Mandibular palp, segment 2 inflated and setose, segment 3 about  $\frac{2}{3}$  length of segment 2. Coxae 1-3, lower posterior corner slit. Gnathopod 1, palm elongate, segments 5 and 6 stout. Gnathopod 2, segment 5 less than twice the length of segment 6. Peraeopod 3, plumose setae confined to distal third of posterior margin of segment 4. Peraeopod 5-6, bases broad, posterior margin of segment 5 bearing 2-3 single spines, posterodistal end of segment 5 produced. Peraeopod 7, lower posterior

corner of basal lobe obliquely rounded, segment 3 longer than 4, segment 4 lacking posterior lobes but bearing a single long plumose setae at lower posterior corner, segment 6 broad and slightly longer than 5, dactyl short and stout. Uropod 1 nearly reaching end of uropod 2, both rami sparsely spinose. Uropod 2, rami shorter than peduncle, medial margins of both rami unarmed. Uropod 3, rami lanceolate and sparsely setose, inner ramus much broader than outer ramus. Telson lobes each tapering to a narrow, laterally notched apex, each notch bearing a single spine, dorsal surface of each lobe with 2-3 small spines in a central row. Pleon sideplate 3, posterior margin convex, ending in a small rounded process at the lower corner. Urosomite 1 only slightly elevated dorsally, without strong carina. Gills (in mature females) flattened and unpleated.

(Male). Pelagic males differ from females in the

presence of brush setae on peduncles of antenna 1 and 2, flagellum setae of both antenna very short. Gnathopod 1, segment 6 narrowed distally so that upper and lower margins are parallel for a third of the segment. Urosomite 1, dorsal surface notched anteriorly and produced posteriorly into a hood-like carina. Uropod 3, rami more setose. Gills less flattened and pleated.

**Remarks:** To date, *A. milleri* has been collected only as far north as the San Francisco Bay region (38°N). The species was treated here since it represents a morphological type not otherwise found in the northeast Pacific, and pelagic males of *A. milleri* were previously undescribed. The shape of pereopod 7 distinguishes *A. milleri* from all other *Ampelisca* in the area (see key p. 3).

***Ampelisca pugetica* Stimpson 1864**

Figure 10.

*Ampelisca californica* Holmes 1908, pp. 513-515, fig. 23

*Ampelisca gnathia* Barnard 1954a, pp. 46-48, pls. 33-34

*Ampelisca pugetica* Barnard 1954a, pp. 49-51, pls. 35-36

**Material examined:** Southeastern Alaska: Bousfield and McAllister stns., 1961; A117, A150 (2 specimens).

British Columbia — Queen Charlotte Islands: J.W. Scoggan stns., 1965; JWS 106 (1 specimen). Bousfield stns., 1957; E11, E14b, E14c, H2, H4a, H5 (50 specimens). North central coast: Bousfield stns., 1964; H5, H13, H25, H50, H53, H57 (20 specimens). Vancouver Island: Bousfield stns.,

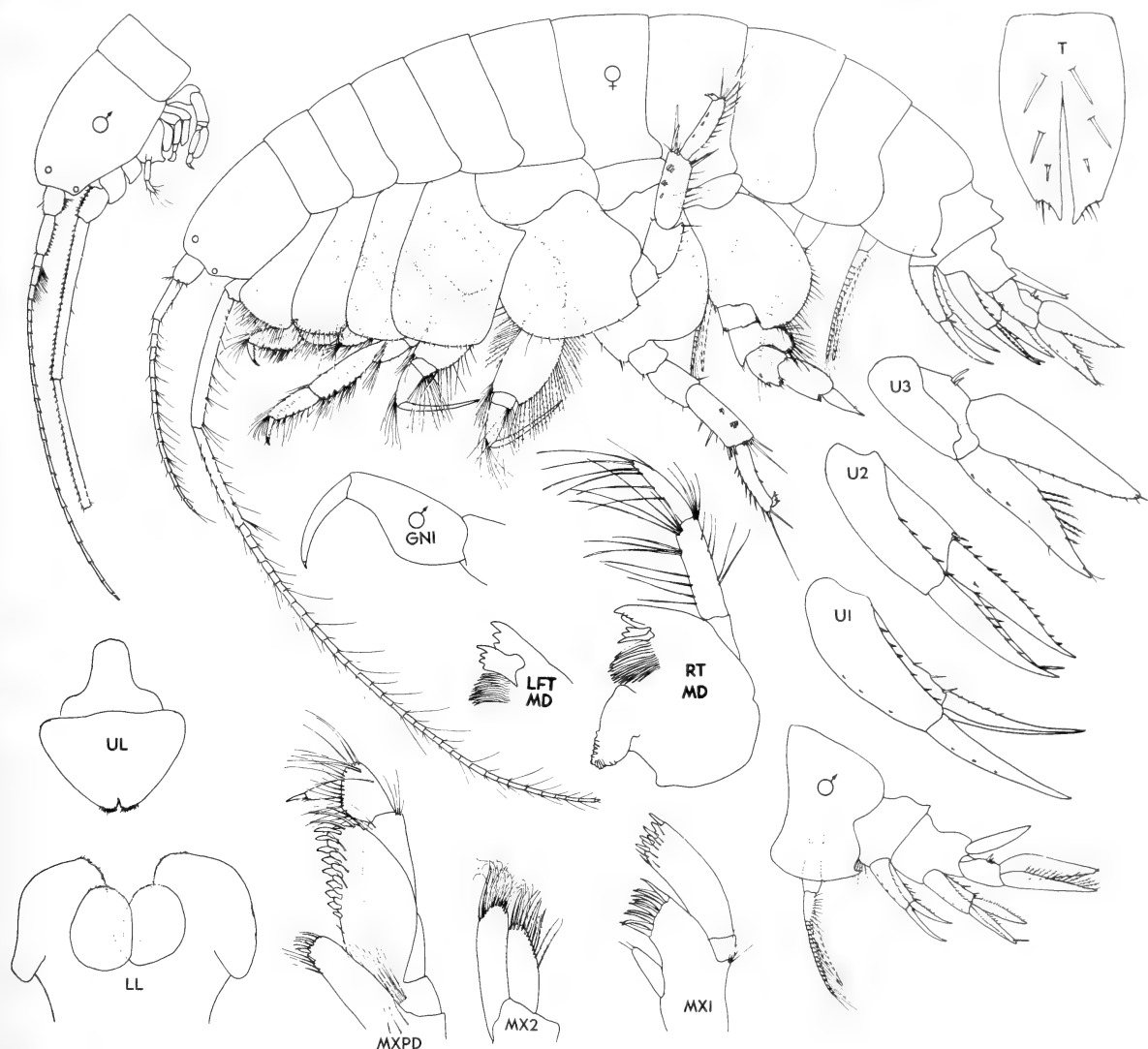


Figure 10. *Ampelisca pugetica* Stimpson. Alert Bay, Vancouver Island, B.C. ♀ 9.0 mm, Los Angeles, California, A. Hancock stn. 5737. ♂ 9.0 mm

1959; N11, N22, V7, V10 (50 specimens). Bousfield stns., 1970; P710b (30 specimens) Bousfield stns., 1975; P17a (25 specimens). Bousfield stns., 1976; B11a, B11b, B26 (12 specimens). Bousfield stns., 1977; B1, B21b, E3 (6 specimens). K. Conlan coll. 1975; Saanich Inlet (3 specimens). D. Ellis coll. 1979; Sidney Channel, Hero Strait (2 specimens).

Southern California: Allan Hancock Foundation stns., 1958; 5737, 33°52'N, 118°31'W, 34.5 fms, sand (13 specimens).

*Distributional Ecology:* Geographic range — Prince William Sound, Alaska (60°28'N, 146°29'W) to Baja California (Barnard 1971a). Bathymetric range — 0-225 m (Barnard 1971a). 0-100 m (NMNS collections). Commonly less than 40 m. Sediment preference — sand bottoms (Barnard 1969b and NMNS coll.).

*Life cycle:* Ovigerous females found in B.C. waters in February (1), July (1), August (2), November (1). Mature males: none in NMNS coll.

*Diagnosis:* (Female). Medium sized *Ampelisca* (9-11 mm) characterized by: head, lower front margin oblique and convex. Antenna 1 short, not reaching end of peduncle of antenna 2, peduncular segment 2 twice the length of segment 1, flagellum setae long. Antenna 2 about body length, flagellum setae long. Mandibular palp, segment 3 slightly more than half as long as segment 2. Coxae 1-2, lower posterior corner slit. Gnathopod 1, palm elongate and relatively deep. Gnathopod 2, segment 6 about half as long as segment 5. Peraeopods 3-4, stout. Peraeopod 3, segment 4 with plumose setae only on distal third of its posterior margin. Peraeopods 5-6, posterior margin of segment 5 with 2-3 sets of comb spines. Peraeopod 7, lower posterior margin of basal lobe rounded, segment 3 subequal to 4 in length, segment 4 with a broad setose posterior lobe extending the length of segment 5, segment 5 with a spine bearing notch on anterior margin, segment 6 inflated and longer than 5 and 7. Uropod 1 short, reaching only halfway along rami of uropod 2, outer ramus armed only with basal spines. Uropod 2, rami shorter than peduncle, both margins of both rami spinulose, outer ramus with long spine at tip. Uropod 3, rami lanceolate, medial margins of both rami setose. Pleon side-plate 3, lower posterior corner bearing a medium-sized tooth. Urosomite 1, dorsal carina saddle-shaped. Telson, each lobe notched and pointed at apex, notch with 2-5 setae, dorsal surface of each

lobe with 3-6 long spines originating centrally. Gills in mature females flattened with a few pleats.

(Male 9.0 mm). A. Hancock stn. 5737. Pelagic stage males differ from females in: presence of brush setae on peduncles of antenna 1 and 2, flagellum setae short. Gnathopod 1, segment 6 narrowing distally so that dorsal and ventral margins are parallel for one-third of segment. Uropods 1-2 more spinulose. Uropod 3 more foliaceous. Urosomite 1 shallower and more rounded dorsal carina. Gills less flattened but more pleated than in females.

*Remarks:* This species is easily identified from other northeastern Pacific *Ampelisca* by its saddle-shaped urosome, the shape of peraeopod 7, and the length of uropod 1 (see key p. 3).

The subspecies *A. pugetica mora* described by Barnard (1967b) from bathyal depths is probably a new species rather than a sub-species and should be re-evaluated. The "macrodentata" form of *A. pugetica* described by Barnard (1954a) from Mexico and Central America was not examined so its status cannot be evaluated here.

*A. pugetica* is represented by two photographs: a ♀ (# AAA pug. 5) from the Burrard Inlet region, and a ♀ (# AAA pug. 4) from the Alexander Archipelago. Both specimens have a yellowish brown ground colour with small areas of red pigment scattered over the peraeopods and uropods. The usual concentration of red pigment is found in the eye region. White pigment chromatophores are found peripheral to the eyes, and scattered over the distal portions of the anterior coxae and peraeopods.

#### *Ampelisca eschrichti* Kroyer 1842

Figure 11.

*Ampelisca eschrichti* Sars 1895, pp. 174-176, pls. 61, fig. 1.

*Ampelisca eschrichti eschrichti* Gurjanova 1955, pp. 167-170, fig. 2.

*Ampelisca eschrichti* Lincoln 1979, p. 118, fig. 50f-j.

*Material examined:* Alaska — Bering Sea: St. Lawrence Island (63°N, 170°W), July 1980, 30-40 m., J. Oliver coll. (25 specimens).

*Distributional ecology:* Geographic range: Circumpolar, through the North Atlantic and Arctic oceans and into the Bering Sea (Stephensen 1935, Dunbar 1954, Gurjanova 1955). Bathymetric range: 0-250 m (Mills 1971). Sediment preference: sand to silt clay (Stephensen 1935).

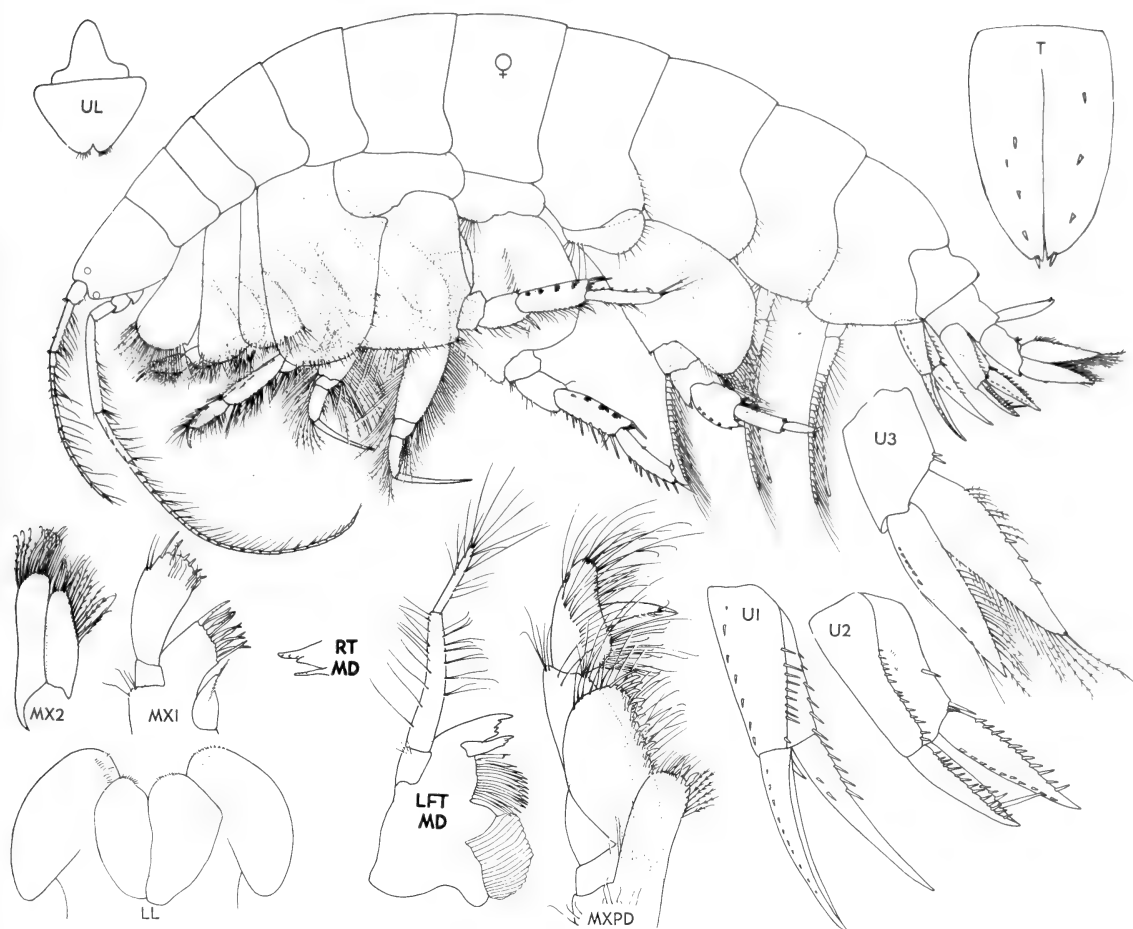


Figure 11. *Ampelisca eschrichti* Kroyer. St. Lawrence Island, Bering Sea, Alaska. ♀ 25 mm, ov.

**Life cycle:** Ovigerous females found in the Bering Sea in July.

**Diagnosis:** (Female). A very large *Ampelisca* (20-30 mm) characterized by: head narrow anteriorly, lower front margin oblique and convex. Antenna 1 extending beyond peduncle of antenna 2, peduncular segment 2 almost three times length of segment 1, flagellum setae long. Antenna 2 about half body length, flagellum setae medium length. Mandibular palp, segment 3 about half the length of segment 2. Maxillipedal palp, segment 3 produced distally well beyond attachment of the dactyl. Coxae 1-2, lower posterior corner toothed. Gnathopod 1, palm elongate. Gnathopod 2, segment 5 twice length of 6. Peraeopod 3, segment 4 with plumose setae along distal  $\frac{2}{3}$  of posterior margin. Peraeopods 5-6, bases broad, segment 5 with 4 rows of comb

spines along posterior margin. Peraeopod 7, basal lobe deep with lower posterior margin oblique nearly straight, segment 3 subequal to 4 in length, segment 4 with a tapering setose posterior lobe, segment 5 with notch in anterior margin, segment 6 long, slender and linear, segment 7 medium length. Uropod 1 short, not reaching end of uropod 2, outer ramus with basal spines only. Uropod 2, outer ramus distinctly shorter than inner ramus and bearing a large tip spine, both margins of both rami spinulose. Uropod 3, rami lanceolate and foliaceous. Telson lobes tapering to rounded apices with a single spine set in a small lateral notch, dorsal surface with 3-4 spines scattered along the central axis of each lobe. Pereonites 6-7 and pleonites 1-3 elevated into a low thin keel along mid-dorsal line. Pleon sideplate 2 slightly

produced at lower posterior corner. Pleon side-plate 3 weakly convex posteriorly, ending in a medium-sized acute tooth. Urosomite 1 produced dorsally to form a massive carina that ends subacutely above urosomite 2. Gills in mature females flattened and unpleated.

(Male). No specimens of pelagic males are present in NMNS collections. Marjorie Bousfield of Dalhousie University kindly loaned me a specimen from Nain Bay, Labrador. The pelagic male differed from the female in: the presence of brush setae on peduncles of antennae 1 and 2, flagellum setae shorter than in female. Urosomite 1 dorsal surface notched anteriorly and produced posteriorly into a hood-shaped carina. Uropods 1 and 2 more spinulose. Uropod 3 more setose. Gills less flattened and strongly pleated.

*Remarks:* The deep water form of *A. eschrichti* found by Barnard (1967a, 1971a) off California and Oregon would seem to merit species recognition based on Barnard's (1971a) illustrations. It

differed from the polar form particularly in the shape of pereopod 7. Gurjanova's (1955) subspecies *A. eschrichti pacifica* is also most likely a separate species although it is difficult to evaluate its status solely from the illustrations.

*Ampelisca eschrichti* is easily identified by its distinctive pereopod 7, telson, and urosomal carina (see key p. 3).

***Ampelisca macrocephala* Liljeborg 1852**

Figure 12.

*Ampelisca macrocephala* G.O. Sars 1895, pp. 172-173, pl. 60, fig. 1.

:Mills, 1967b, pp. 640-642, fig. 2.

:Bousfield 1973, pp. 133-134, pl. 36, fig. 1

:Lincoln 1979, p. 118, fig. 50a, - e.

*Material examined:* Alaska — Bering Sea: St. Lawrence Island (63°N, 169°W), 40 m, July 1980 (30 specimens). Beaufort Sea: (70°43'N, 149°2'W), 50 m, 6 September 1971 (2 specimens).

*Diagnosis:* (Female). A large *Ampelisca* (15-24

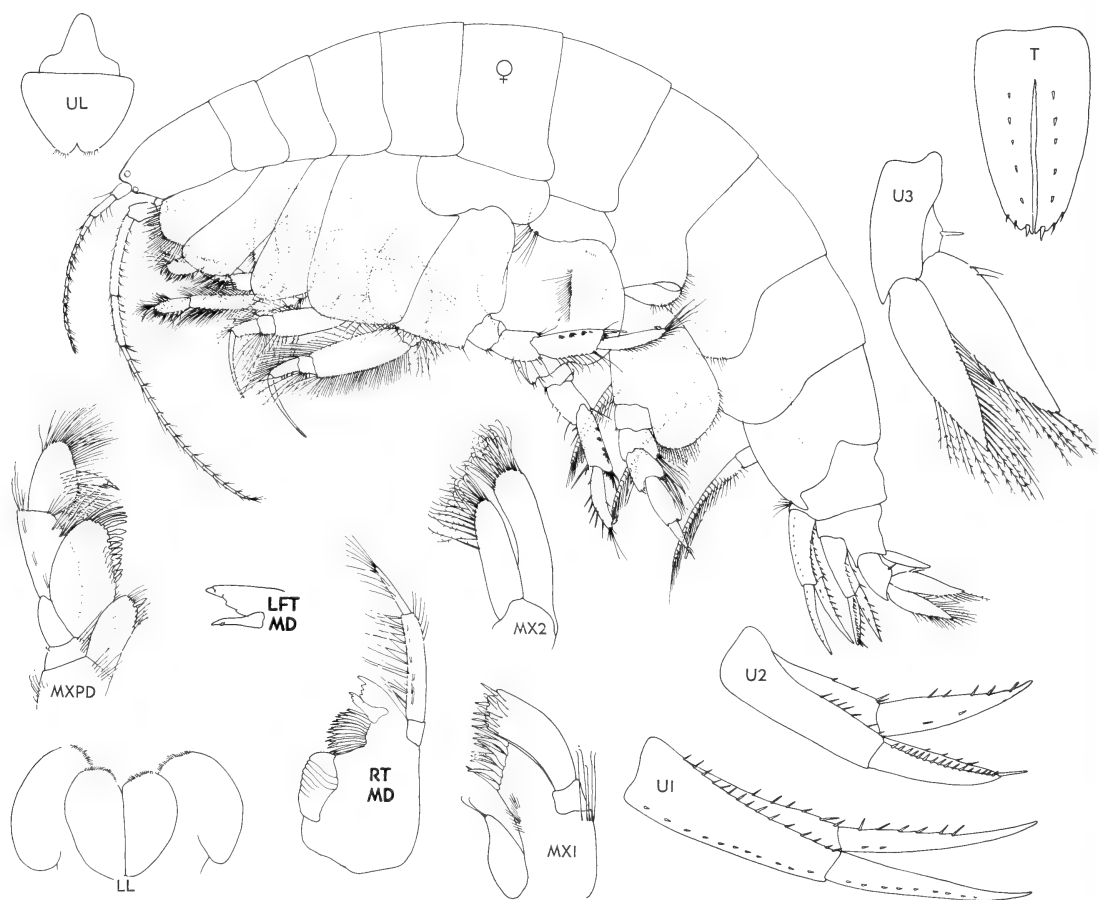


Figure 12. *Ampelisca macrocephala* Liljeborg. St. Lawrence Island, Bering Sea, Alaska. ♀ 22 mm, ov.

mm) characterized by: head, upper front margin produced slightly forward; lower front margin oblique, slightly concave under lower eye continuing convexly to insertion of antenna 2. Eyes present. Antenna 1 short just reaching end of peduncle of antenna 2, peduncular segment 2 variable in length but less than twice segment 1, flagellum setae short. Antenna 2 about half body length, flagellum setae short. Mandibular palp, segment 2 about twice length of segment 3. Coxae 1-2, lower posterior corner toothed. Coxa 3, tooth absent in Bering Sea and Beaufort Sea populations, tooth present in Northwest Atlantic populations. Gnathopod 1, palm short, less than one third length of segment 6. Gnathopod 2, segment 6 about half length of segment 5. Peraeopod 3, plumose setae confined to distal half of posterior margin of segment 4. Peraeopods 5-6, posterior margin of segment 5 with 4-5 rows of comb spines. Peraeopod 7, basal lobe deep, lower posterior margin obliquely rounded, segment 3 subequal to 4 in length, segment 4 with tapering, setose, posterior lobe which extends about halfway down segment 5, segment 6 much longer than 5, segment 7 subequal to 5 in length. Uropod 1 reaching tip of uropod 2, outer ramus with basal spines only. Uropod 2, rami shorter than peduncle, outer ramus slightly shorter than inner ramus with long sub-apical spine, both margins of both rami spinulose. Uropod 3, rami slender, lanceolate and foliaceous. Telson lobes tapering to laterally notched apices, notch bearing blunt spine and short seta, apices in large specimens (20-25 mm) bear 1-2 spines on distal lateral margins, dorsal surface of each lobe with 5-6 short blunt spines in central row, additional spines occasionally near lateral margins. Pleon sideplate 3, posterior margin convex, ending in a large acute tooth. Urosomite 1 weakly elevated dorsally to form a massive saddle-shaped carina. Gills in mature females flattened and unpleated.

(Male). No specimens in NMNS collections. Sars (1895) showed the pelagic male to differ in: the presence of brush setae on the peduncles of the antenna 1 and 2; antenna 1 longer than in the female and extending beyond peduncle of antenna 2. Urosomal carina more strongly developed.

*Distributional ecology:* Geographic range: Boreal North Atlantic through Arctic Ocean into the Bering Sea (Mills 1967b). Bathymetric range:

10-280 m (Mills 1967b). Sediment preference: sand bottoms (Dickinson *et al.* 1980).

*Life cycle:* It takes 18 months to reach breeding age in fall of the second year. Males then die after breeding. Females carry embryos ( $\bar{x} = 60$ ) 5 months over winter. Juveniles released in spring. Most females then die (2 years old), but a few live on and breed again to reach 3 years (Kannevorf 1965).

*Remarks:* This species is very similar to *Ampelisca careyi* n.sp. (see phenogram fig. 21). However, these two species may be reliably separated by their armature patterns on the dorsal surface of the telson and size at maturity.

### *Ampelisca careyi* n.sp.

Figure 13

*Ampelisca macrocephala* Barnard 1954a, pp. 41-43, Fig. 29.

*Material examined:* Southeast Alaska — Alexander Archipelago: Bousfield stns., 1980; S18F2, S18F3 (2 specimens).

British Columbia — Queen Charlotte: Bousfield stns., 1957; H3 (20 specimens).

North Central Coast: Bousfield stns., 1964; H13, H17, H27, H31, H34, H36, H37, H49 (75 specimens). C. Levings, Swanson Bay stns., 1973; 28, 29 (4 specimens). C. Levings, Swanson Bay stns., 1975; 53°00'N, 128°30'W, 18 November 1975, 62 m; holotype ov. ♀, 10 mm (NMC-C.1981-381); allotype mat. ♂, 8 mm (NMC-C.1981-382), 6 ♀ ♀, 4 ♂ ♂, 8 imm. paratypes (NMC-C.1981-383). Vancouver Island: Bousfield stns., 1970; P717 (1 specimen), Bousfield stns., 1975; P10, P21a, P22 (4 specimens). Bousfield stns., 1976; B26, B28 (6 specimens). Bousfield stns., 1977; B16, B18, B21a (4 specimens). Southern Mainland: Bousfield stns., 1977; P3 (10 specimens). Bousfield stns., 1978; V4 (20 specimens). Oregon — OSU coll. 01248, 44°26.1'N, 124°14.5'W, 21 June 1976, 62 m (2 specimens).

California — A. Hancock Found. 5270, 34°20'N, 119°53'W, 3 November 1957, 45 m, (7 specimens).

*Distributional ecology:* Geographic range — Southeast Alaska (55°N) to Baja California (Barnard 1971a). Bathymetric range: 0-200 m primarily shallower than 100 m (NMNS coll.). Sediment preference: sand.

*Life cycle:* Ovigerous females found in B.C. waters in the months of March (1), May (1), June (1), July (30), August (2), November (16), December (1). Pelagic males: June (2), July (1),

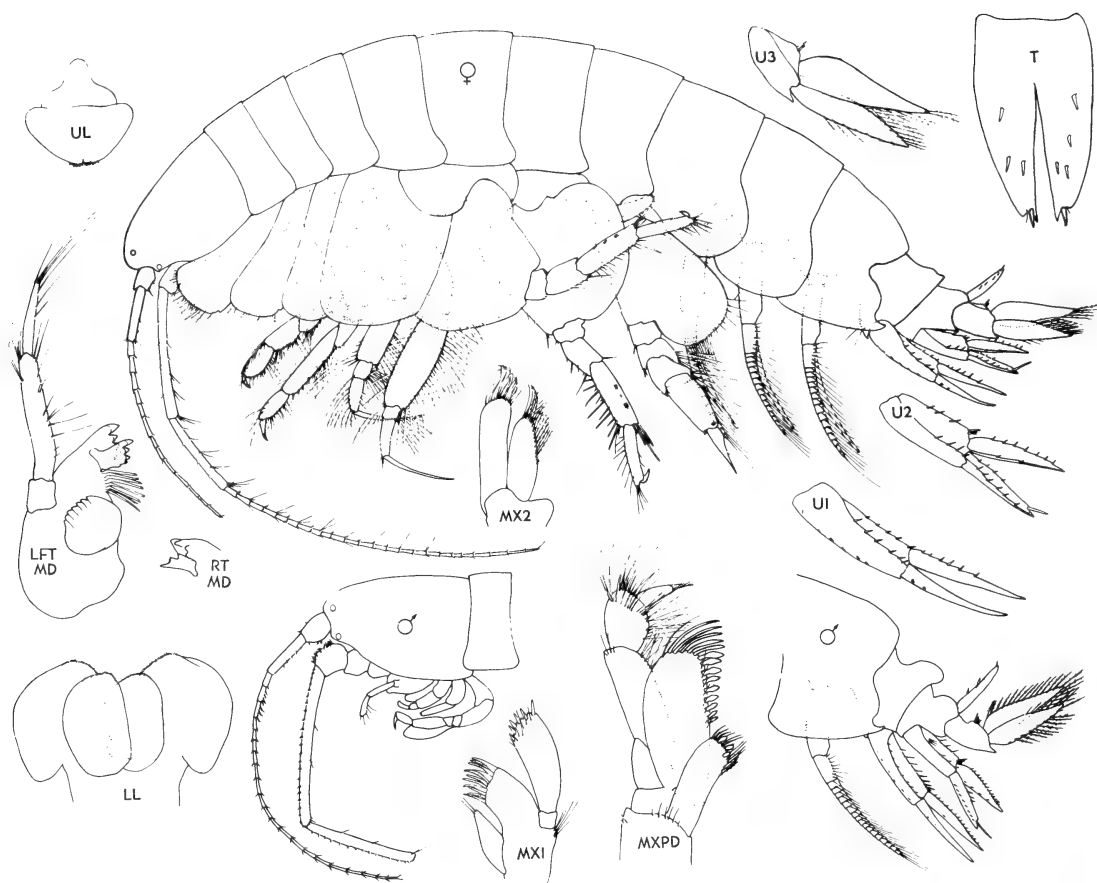


Figure 13. *Ampelisca careyi* n.sp. Swanson Bay, B.C. Paratype ♀ 8 mm. Paratype ♂ 8 mm

August (1), November (2). This species must have a different life cycle than that described by Kanneworf (1965) for *A. macrocephala* since ovigerous females are present throughout the summer months.

**Diagnosis:** (Female). A medium sized *Ampelisca* (7-12 mm) characterized by: head, produced anteriorly into a dome-shaped process above antenna 1, lower front margin distinctly concave. Eyes present. Antenna 1 extending just beyond end of peduncle of antenna 2, peduncular segment 2 more than twice length of segment 1, flagellum setae short. Antenna 2 about  $\frac{2}{3}$  body length, flagellum setae short. Mandibular palp, segment 2 about twice length of segment 3. Coxae 1-3, lower posterior corner slit to form small tooth. Gnathopod 1, palm short, extending less than one-third the length of segment 6. Gnathopod 2, segment 5 about twice length of segment 6. Peraeopod 3, plumose setae confined

to distal half of posterior margin of segment 4. Peraeopod 5-6, segment 5 with 2-3 sets of comb spines on posterior margin. Peraeopod 7, basal lobe deep with lower posterior margin obliquely rounded, segment 3 subequal to 4 in length, segment 4 with tapering setose posterior lobe which extends about half the length of segment 5, segment 6 much longer than 5, segment 7 subequal to 5 in length. Uropod 1 reaching end of uropod 2, outer ramus with basal spines only. Uropod 2, rami shorter than peduncle, outer ramus shorter than inner, with long sub-apical spine, both margins of both rami spinulose. Uropod 3, rami slender, lanceolate, and foliaceous. Pleon sideplate 3, posterior margin convex, ending in short acute tooth. Urosomite 1 elevated into a saddle-shaped carina ending acutely above urosomite 2. Telson lobes tapering to laterally notched apices, notches each armed with a spine and setule, dorsal surface of each lobe bearing



3-4 scattered long slender spines. Gills flattened and unpleated in mature females.

(Male). Pelagic males are characterized by: presence of brush setae on peduncles of antenna 1 and 2, flagellum setae shorter than in female; urosomal carina large and hood-shaped; uropods 1-2 more spinulose; uropod 3 more setose; gills less flattened and strongly pleated.

*Remarks:* *A. careyi* n.sp., is very similar to both *A. macrocephala* and *A. unsocalae* (see phenogram fig. 21). However, it is distinct from *A. macrocephala* on the basis of its telson armature. *A. careyi* and *A. unsocalae* differ in head shape, length of tooth on pleon sideplate 3, relative length of antenna 1, and the position of the apical notch in the telson (see key p. 3 and figs. 13-14).

*A. careyi* is represented by six photographs: 2 ♀♀ (#AAA car. 4, #AAA car. 9) from the Alexander Archipelago region and 2 ♂♂ (#AAA car. 5, #AAA car. 8) and 2 ♀♀ (#AAA car. 6, #AAA car. 7) from the Barkley Sound region. The cuticular ground colour varies from translucent to off-white to yellow brown among the specimens. This species is relatively heavily pigmented. In typical pattern, red pigment spots are found in solid or reticulated masses interrupted along the dorsal line and on all the appendages and epimeral plates. The mid portion of the body above the body-coxae junction line shows the least pigmentation. The anterior portion of the head shows the usual concentration of red pigment around the eyes; the number of white pigment chromatophores varies between specimens, but the pigment is always concentrated in a dorsoventral band between the frontal and caudal eyes. Some of the specimens have banding of white pigment on the distal segments of the gnathopods and pereopods 3 and 4, but in other specimens the white pigment spots are scattered or lacking on these appendages. The male specimens have larger masses of red pigment associated with the eyes than found in the females. Other species of *Ampelisca* photographed in the Gulf of Mexico region, *A. verrilli* (#AAA ver. 7, #AAA ver. 8) and *A. agassizi* (#AAA aga. 9, #AAA aga. 10) show this same pattern suggesting that this male-female difference in pigmentation of the eyes may be typical in *Ampelisca*.

*Etymology:* This species is named in honour of A.G. Carey of Oregon State University who is an active researcher in marine benthic ecology and kindly loaned a great deal of valuable

material from his collections of amphipods from Oregon coastal waters.

*Ampelisca unsocalae* J.L. Barnard 1960 new status Figure 14.

*Ampelisca macrocephala unsocalae* Barnard 1960, pp. 28-30, fig. 7.

*Material examined:* British Columbia — Queen Charlotte Islands: J.W. Scoggan coll. 1965; Dixon Entrance, stns., 104, 105 (90 specimens). North Central Coast: NMNS coll. 1967; 51°23'N, 129°08'W, 175 m, 14 August 1967 (2 specimens). Vancouver Island: NMNS coll., 48°21', 126°08'W, September 1968 (1 specimen). Southern Mainland: Bousfield stns., 1977; J2, P3, P4, P6, P7, P8 (40 specimens). Bousfield stns., 1978; V5, V6 (100 specimens).

Oregon — Oregon State University Benthic Invertebrate coll. 01332, 44°34.2'N, 124°52.6'W, 16 June 1963, 600 m, identified by J.L. Barnard (1 specimen).

California — A. Hancock Foundation stn., 6915, 33°59'N, 118°48'W, 13 March 1960, 250 m (13 specimens).

*Diagnosis:* (Female). A medium-sized *Ampelisca* (7-9 mm) characterized by: head, upper front margin not produced forward, lower front margin oblique and convex. Antenna 1 short, not reaching end of peduncle of antenna 2, peduncular segment 2 about twice length of segment 1, flagellum setae short. Antenna 2 about body length, flagellum setae short. Mandibular palp, segment 3 about half length of segment 2. Coxae 1-3, small tooth on lower posterior corner. Gnathopod 1 palm short, less than  $\frac{1}{3}$  of posterior margin of segment 6. Gnathopod 2, segment 5 about twice length of segment 6. Pereopod 3, plumose setae along distal  $\frac{2}{3}$  of posterior margin of segment 4. Pereopod 5-6, posterior margin of segment 5 with 3 sets of comb spines. Pereopod 7, basal lobe deep, segment 3 subequal to 4 in length, segment 4 with tapering setose posterior lobe extending half the length of segment 5, segments 5 and 7 subequal in length, segment 6 much longer than 5. Uropod 1 reaching end of uropod 2, outer ramus with basal spines only. Uropod 2, rami longer than peduncle, outer ramus shorter than inner and with a long sub-apical spine, both margins of both rami spinulose. Uropod 3, rami slender, lanceolate and foliaceous. Telson lobes tapering to a centrally notched apex bearing a spine and setule, dorsal surface of each lobe bearing 5 long scattered

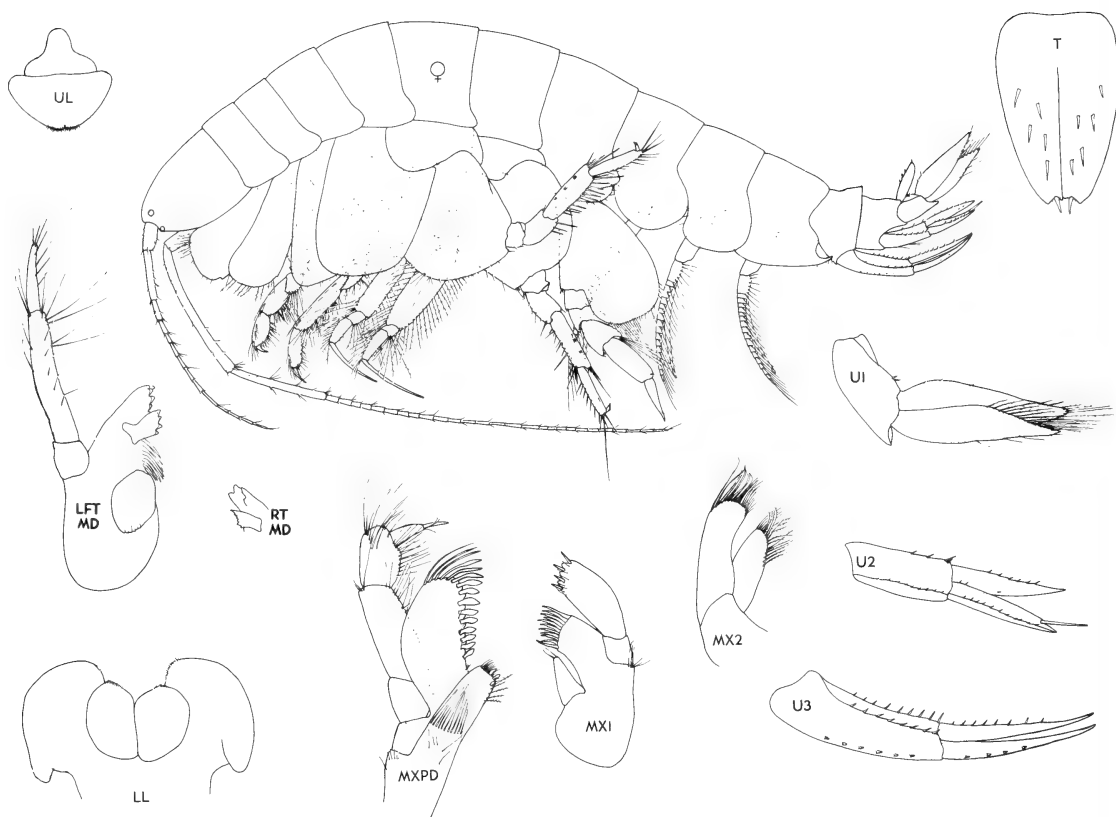


Figure 14. *Ampelisca unsocalae* J.L. Barnard. Dixon Entrance, Queen Charlotte Islands, B.C. ♀ 9 mm, ov.

spines. Pleon sideplate 3, posterior edge convex, ending in a long slender tooth. Urosomite 1 elevated into a carina which rises posteriorly to a right angle above urosomite 2. Gills flattened and unpleated in mature females.

(Male 7.0 mm). The pelagic male is characterized by: the presence of brush setae on peduncles of antennae, the relative lengths of antennae are unknown since the flagellae are broken on available specimens; urosomite 1 is produced dorsally into a hood-shaped carina; uropod 3 is more setose.

**Distributional ecology:** Geographic range: Queen Charlotte Islands to southern California (Barnard 1971). Bathymetric range: 50-1700 m (Barnard 1971). Primarily, 100-400 m (NMNS coll.). Sediment preference: silt to silt-clay bottoms.

**Life cycle:** Ovigerous females found in B.C. waters during the months of May (1), July (8),

August (13), September (1), November (25). Pelagic males: July (1), August (2).

**Remarks:** Barnard (1960) described this species as a subspecies of *A. macrocephala* which lost its eyes in deeper water (400 m). However, the differences in morphology including head shape, relative antennal lengths, shape of tooth of pleon sideplate 3, and shape of apical notch of the telson warrant full species recognition. The majority of the specimens in the NMNS were collected between 100-400 m and have eyes; specimens collected from greater depths (600 m) off Oregon lack eyes but seem otherwise identical.

*Ampelisca unsocalae* is represented by photographs of three ♀ specimens (#AAA uns. 3, #AAA uns. 4, #AAA uns. 5) from the Burrard Inlet region. All three specimens show a basically transparent body with faint traces of red pigment particularly in the buccal mass and on the bases of pereopods 5-7. The anterior portion of the

head has the usual concentration of red pigment near the eyes with white pigment granules concentrated between the frontal and caudal eyes. The distal edges of coxae 1-2 and the distal segments of the gnathopods and pereopods 3-4 also have scattered white pigment chromatophores.

***Ampelisca cristata* Holmes**

Figure 15.

*Ampelisca cristata* Holmes 1908, pp. 507-508, figs. 16-17.

Barnard 1954a, pp. 26-28, pls. 17a-d, 18a, c, d, f, g.

**Material examined:** Southeast Alaska — Alexander Archipelago: Bousfield and McAllister stns., 1961; A169 (1 specimen).

British Columbia — North Central Coast: Bousfield stns., 1964; H52 (2 specimens). C.

Levings stns., Swanson Bay, 1973; (51B-031), 1975; (51B-013) (2 specimens); Vancouver Island: Bousfield stns., 1977; B13 (1 specimen).

Southern Mainland Coast: Bousfield stns., 1955; M1 (1 specimen). Bousfield stn., 1959; N22 (1 specimen).

Oregon: Oregon State University Benthic Invert. coll. 01257, 44°10'N, 124°14.7'W, 24 June 1976 (1 specimen).

**Distributional ecology:** Geographic range — Alexander Archipelago (56°16'N, 135°30'W) to Costa Rica (Barnard 1954a). Bathymetric range: 0-152 m (Barnard 1971a), 0-70 m (NMNS coll.). Sediment preference: coarse sand.

**Life cycle:** No ovigerous females or pelagic males in NMNS collections.

**Diagnosis:** (Female). A large *Ampelisca* (12-17 mm) characterized by: head long, narrowing anteriorly, lower front margin parallel to upper

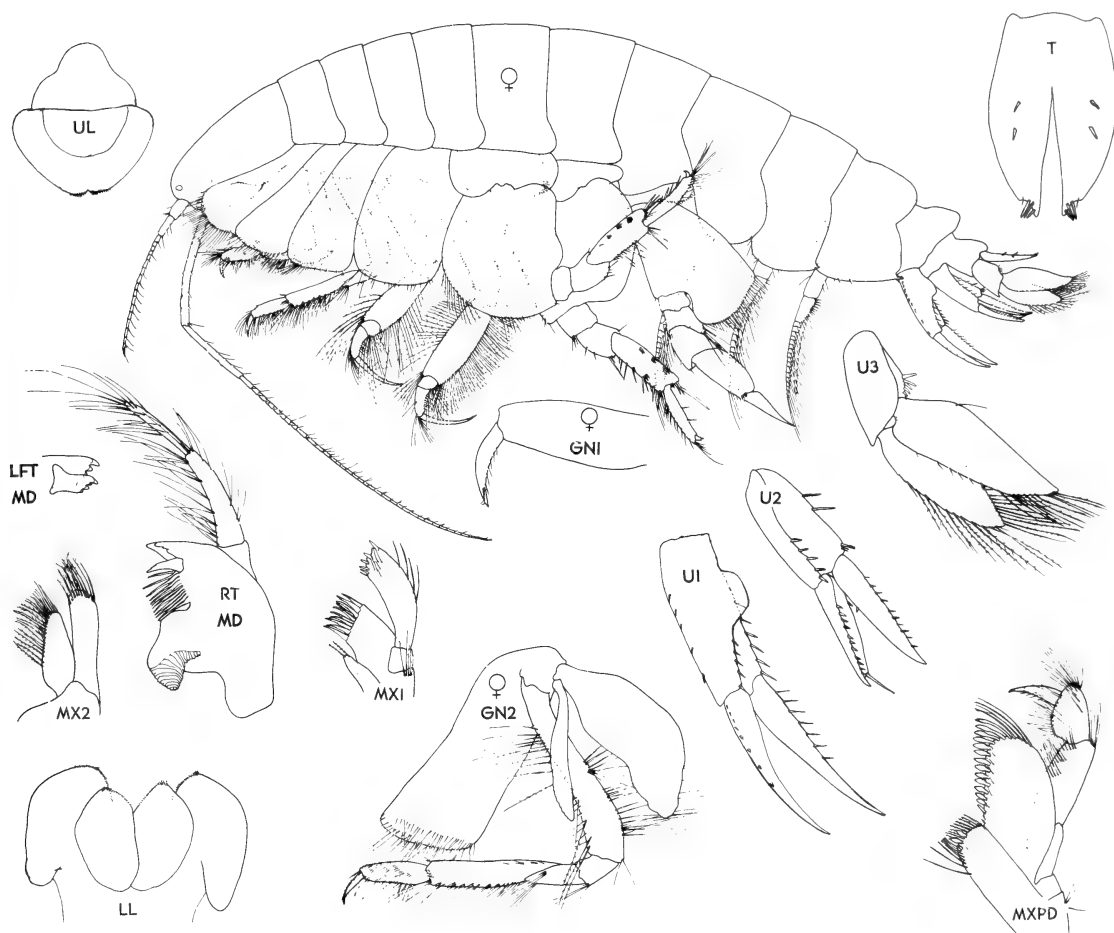


Figure 15. *Ampelisca cristata* Holmes. Swanson Bay, B.C. ♀ 10 mm, br. II

margin. Antenna 1 short, not reaching end of peduncle of antenna 2, peduncular segments 1-2 subequal in length, flagellum setae medium length. Antenna 2 about  $\frac{3}{4}$  body length, flagellum setae medium length. Mandibular palp, segment 3 about  $\frac{2}{3}$  length of segment 2. Maxilla 1, segment 2 of palp with setae along distal portion of outer margin. Coxa 1, small tooth at lower posterior corner. Gnathopod 1, palm shallow and elongate. Gnathopod 2, segment 5 more than twice length of segment 6. Peraeopod 3, segment 4 with plumose setae along distal  $\frac{2}{3}$  of posterior margin. Peraeopods 5-6, segment 5 with 3-4 sets of comb spines along posterior margin. Peraeopod 7, lower posterior margin of basal lobe oblique nearly straight, segment 3 shorter than 4, segment 4 with small slender setose posterior lobe, segment 6 inflated and longer than 5 and 7. Uropod 1, nearly reaching end of uropod 2, middle portion of upper margin of peduncle elevated into a lamellar carina, outer ramus with basal spines only. Uropod 2, rami shorter than peduncle, outer ramus with long tip spine, both margins of both rami spinulose. Uropod 3, rami broadly lanceolate and foliaceous. Telson lobes, notched laterally and pointed medially at tip, notches bearing 3-4 spines and 1 setae, dorsal surface with 2-4 pairs of medium length spines originating centrally. Pleon sideplates 2-3, tooth at lower posterior corner, dorsal surface of pleonite 3 elevated into two low longitudinal crests. Urosomite 1, dorsal surface elevated into lamellar carina. Gills flattened in mature females with a few indistinct pleats.

(Male). Unknown.

*Remarks:* *Ampelisca cristata* is easily distinguished from other Northeast Pacific ampeliscids by its head shape and urosomal carina (see key p. 3).

The status of Barnard's (1954b) records from the Caribbean and form "microdentata" (Barnard 1954a) could not be evaluated from his limited illustrations.

A single photograph of *A. cristata* (#AAA cri. 4) shows the colour patterns in a ♀ specimen from the Barkley Sound region. The body is basically translucent, but small amounts of red pigment dot the dorsal surface of the thorax, the antennae, peraeopods, and uropods. The anterior portion of the head is heavily pigmented in red and white. The red pigment is concentrated around the eyes in the usual manner. The white pigment is concentrated in a band between the

frontal eyes, but scattered pigment spots occur over the entire anterior half of the head and distal portions of coxae 1 and 2.

### *Ampelisca brevisimulata* J.L. Barnard

Figure 16.

*Ampelisca brevisimulata* Barnard 1954a, pp. 33-35, pls. 23-24.

*Material examined:* Alaska — Bousfield and McAllister stns., 1961; A42, Lynn Canal, 58°31'N, 134°50'W (1 specimen). N.A. Powell coll. 1969; Izembek Lagoon, 55°20'N, 162°55'W (1 specimen).

British Columbia — Queen Charlotte Islands: J.W. Scoggan coll. 1965; 104, 105 (3 specimens). North Central Coast: Bousfield stns., 1964; H34 (1 specimen). C. Levings stns., Swanson Bay, 1973; (1 specimen), 1975; (8 specimens). Vancouver Island: D. Ellis coll., 1965; Parry Bay, 48°23'N, 123°30'W (1 specimen). Bousfield stns., 1975; P13 (1 specimen). Bousfield stns., 1976; B10a (1 specimen). NMNS coll., Numukamis Bay, 48°55'N, 125°00'W (1 specimen). Southern Mainland: Bousfield stns., 1977; E1 (1 specimen). Bousfield stns., 1978; V6 (2 specimens). Washington — Lopez Island: Upright Head, R.I. Smith coll. 1955; (1 specimen).

Oregon — Oregon State University Benthic Invertebrate coll. 43°49'N, 124°50'W, 417 m, 28 June 1976; 46°06'N, 124°13'W, 88 m, 1 October 1974 (3 specimens).

*Distributional ecology:* Geographic range — Southeast Alaska (58°30'N, 134°50'W) to Panama (Barnard 1971). Barnard (1954b) also reported it from the Caribbean Sea, but he did not illustrate it from that region. Bathymetric range: 20-400 m (NMNS coll.). Sediment preference: sand to silt clay.

*Life cycle:* Ovigerous females found in B.C. waters during the months of January (1), May (1), November (1). Pelagic males: November (2).

*Diagnosis:* (Female). Medium-sized *Ampelisca* (7-9 mm) characterized by: head, lower front margin concave almost parallel to upper margin. Antenna 1 short, not reaching end of peduncle of antenna 2, peduncular segment 2 more than twice length of segment 1, flagellum setae short. Antenna 2 about  $\frac{2}{3}$  body length, flagellum setae short. Mandibular palp, segment 3 about  $\frac{2}{3}$  length of segment 2. Coxae 1, small tooth at lower posterior corner. Gnathopod 1, palm shallow and elongate. Gnathopod 2, segment 5 more than twice length of segment 6. Peraeopod 3,

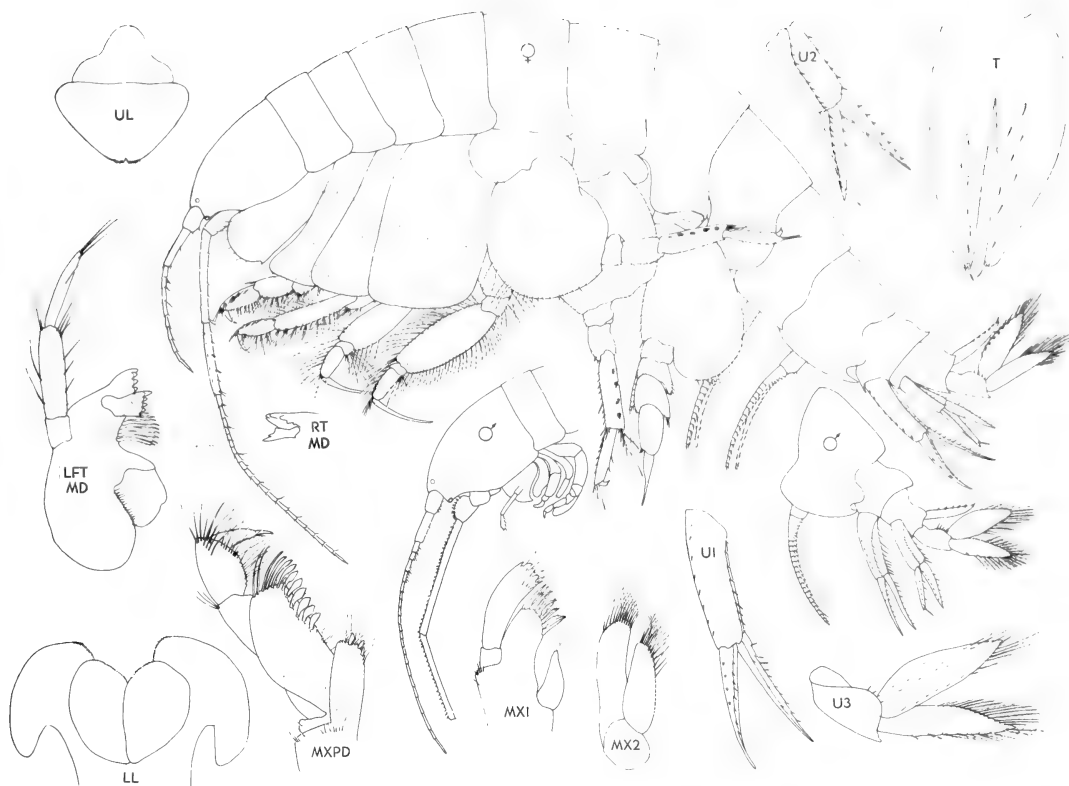


Figure 16. *Ampelisca brevisimulata* J.L. Barnard. Cape Beale, Vancouver Island, B.C. ♀ 7 mm, ov.; Burrard Inlet, B.C., ♂ 6 mm

plumose setae restricted to distal third of posterior margin of segment 4. Peraeopods 5-6, segment 5 with 4-5 sets of comb spines on posterior margin. Peraeopod 7, lower posterior margin of basal lobe rounded, segment 3 subequal to 4 in length, segment 4 bearing a slender setose posterior lobe, segments 5 and 6 inflated, segment 6 relatively short just slightly longer than 5, segment 7 slender and subequal to 6 in length. Uropod 1 long, extending beyond end of uropod 2, both rami spinulose. Uropod 2, rami subequal to peduncle in length, outer ramus with tip spine, inner ramus unarmed along medial margin. Uropod 3, rami broad, lanceolate and foliaceous. Telson lobes tapering to narrow apices, each bearing 1-2 setae, dorsal surface bearing 6-12 scattered setae. Pleon sideplate 2, small acute tooth at lower posterior corner. Pleon sideplate 3, large tooth at lower posterior corner, produced

into a large, rounded hump above the tooth. Urosomite 1 slightly produced dorsally, ending acutely above urosomite 2. Gills flattened and unpleated in mature females.

(Male). Pelagic males differ from females in: the presence of brush setae on peduncles of both antenna; antenna 1 longer than in female, extending beyond peduncle of antenna 2; flagellum setae of both antenna very short. Pleon sideplate 3, tooth smaller, not as long as process above it. Urosomite 1 produced more dorsally into a hood-shaped carina. Uropods 1-2 slightly more spinose. Gills moderately pleated and less flattened.

*Remarks:* Mature specimens of *A. brevisimulata* are easily distinguished from other Northeast Pacific *Ampelisca* by the shape of the head, pleon sideplate 3 and the telson (see key p. 3). Juveniles of *A. brevisimulata* could be confused with other

species in the *A. macrocephala* group, but it seems recognizable at all sizes by its head shape. Based on its telson, uropod 3, and pereopod 7, *A. brevisimulata* shows a strong similarity to Atlantic species such as *A. verrilli*, *A. holmesi* and *A. brevicornis*.

### Discussion

The coxal gills of Ampeliscidae are rarely illustrated and seldom described in taxonomic treatments of the group. Although Sars (1895) illustrated a representative gill of one species for each of his three Norwegian genera, *Ampelisca*, *Byblis*, and *Haploops*, subsequent major works on the Ampeliscidae such as Reid (1951), Barnard (1954a), Karaman (1975) and Bellan-

Santini and Kaim Malka (1977) make little or no mention of gill structure. However, Mills (1963, 1964, 1967b) described and illustrated the gills of some species from the western Atlantic. The present study revealed gill structure varied among species of *Ampelisca*, and that sexual dimorphism typified all species and was rather striking in most.

The species of *Ampelisca* from the northeast Pacific could be divided into two groups on the basis of gill structure. The first type of gill resembles an upside-down conifer tree when viewed in longitudinal section and will be referred to as the "dendritic" type of gill in this paper (see Fig. 17). The surface of the gill lamellae of this type has a series of folds perpendicular to the long axis of the gill. In longitudinal

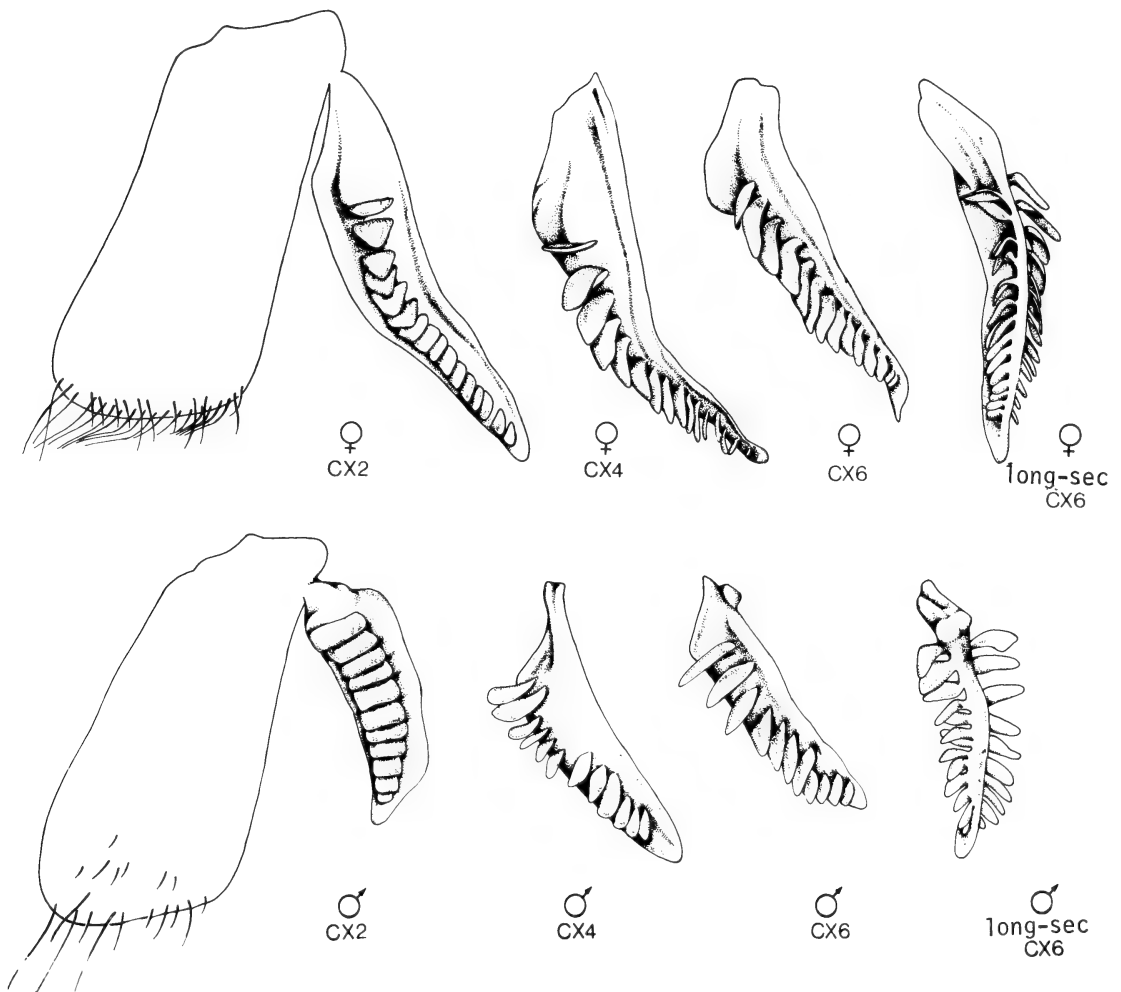


Figure 17. Coxal gills of *Ampelisca agassizi* from coxae 2, 4, 6 for ♀ 11 mm, ov., and ♂ 7 mm, subadult

section, these folds can be seen to originate opposite each other on either side of the gill. Internally, the tissue of the gill folds is reticulated with tiny anastomosing spaces presumably to maximize the surface area for respiratory exchange. The gills of mature females are longer and more slender, with shorter and narrower folds than in males and juvenile females. The folds of the female gill curve downward so the folds overlap against the axis of the gill. Thus, female gills tend to appear much thinner in longitudinal section than in the male where the folds are nearly perpendicular to the gill axis for their entire length. When viewed laterally (as attached to the coxae), the gills of the male often appear twisted on their peduncles so that the longitudinal rather than facial view is presented. Gill form changes little from coxae 2-6, but the size varies somewhat with coxal gill 6 usually the smallest. This type of gill structure is found in *A. agassizi*, *A. fageri*, *A. hancocki*, and *A. lobata* (Fig. 18). Within this group, *A. lobata* has more and relatively longer gill folds than the other three. In *A. agassizi*, females have relatively longer and more slender gills than those of the other three species. The small size of *A. hancocki*

and the scarcity of specimens of *A. fageri* rendered comparisons difficult with the other two species and were not done here.

The second type of gill is referred to as the "pleated" type. Males in this species group have gills with a series of shallow, relatively broad folds or pleats which form a venetian blind-like structure in a facial view (see Fig. 19). The male gill is broad at the base and tapers distally to a rounded apex. The pleats are reticulated with tiny anastomosing spaces. The outer margin of the gill is translucent. In cross section, the pleats of the male gill can be seen to originate in alternate fashion on the two faces of the gill, and that the gill tapers distally. Mature females of this group have gills which are longer, narrower, thinner, and usually unpleated or occasionally weakly pleated. As in the male, the gills of females have a translucent outer margin with a central area of reticulated respiratory tissue. In form, the gills show little change from coxae 2-6, but in size coxal gill 4 is longest and coxal gill 6 is shortest (Fig. 19). This type of gill structure is found in *A. birulai*, *A. brevisimulata*, *A. careyi*, *A. cristata*, *A. eschrichti*, *A. hessleri*, *A. macro-*

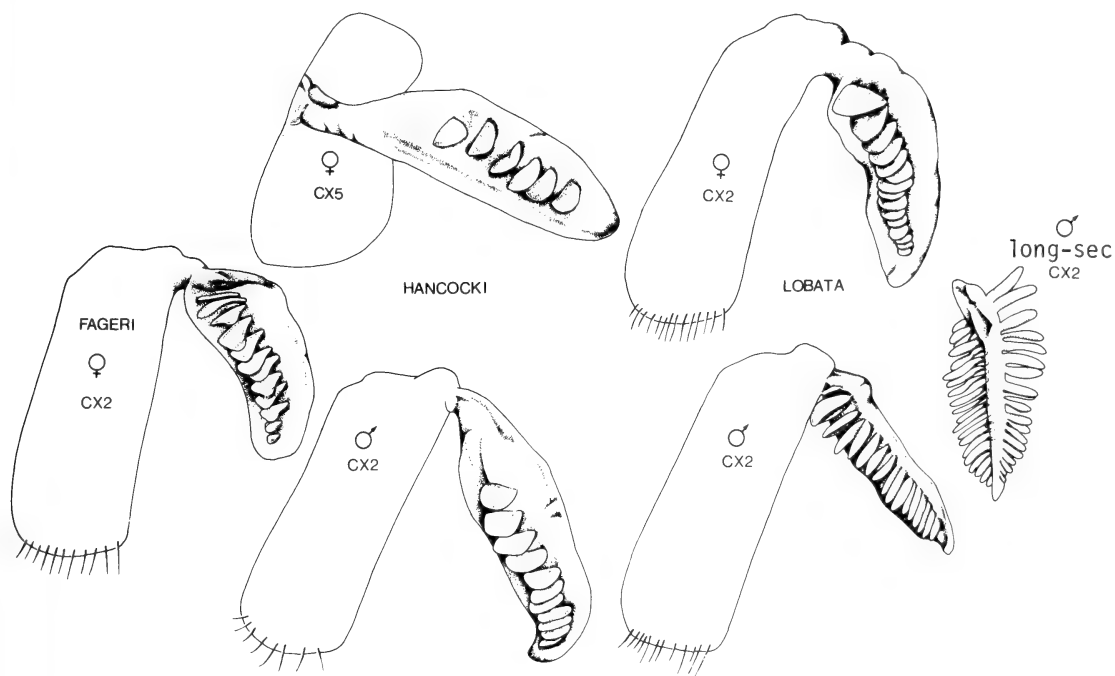


Figure 18. Representative coxal gills of *Ampelisca fageri*, ♀ 8 mm, br. II, *Ampelisca hancocki*, ♀ 5 mm, ov., ♂ 4 mm, subadult, and *Ampelisca lobata*, ♀ 7 mm, ov., ♂ 6 mm, subadult

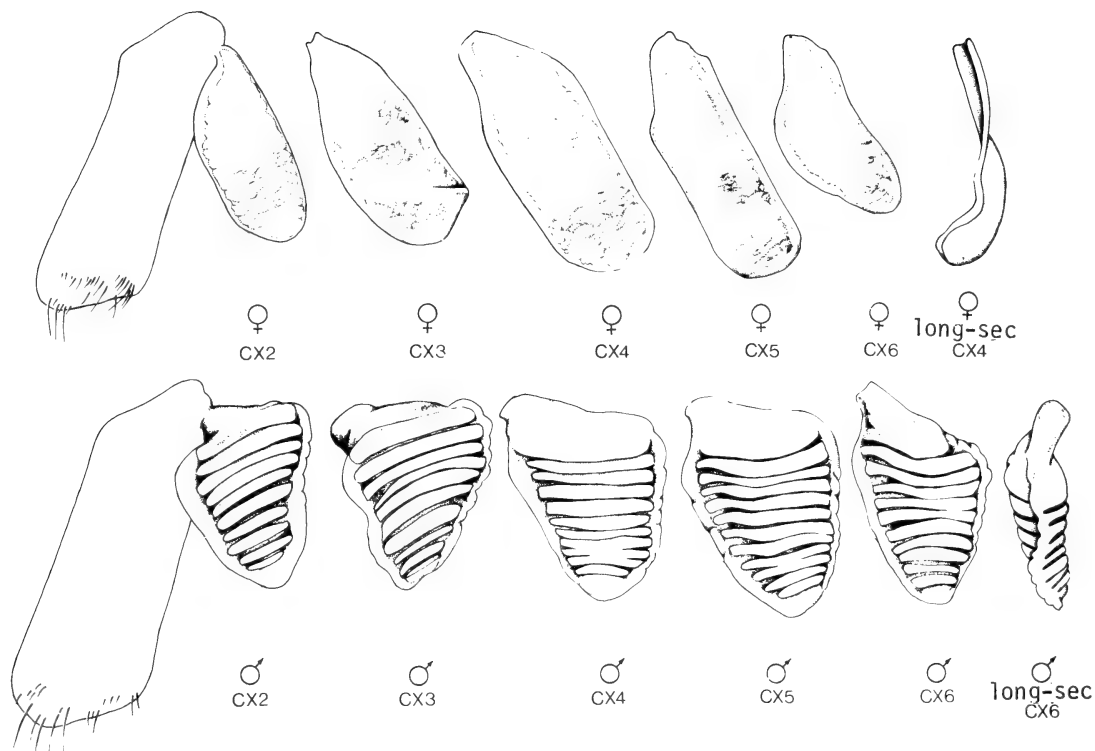


Figure 19. Coxal gills of *Ampelisca macrocephala* from coxae 2-6 for ♀ 20 mm, ov., and ♂ 20 mm, subadult.

*cephala*, *A. milleri*, *A. plumosa*, *A. pugetica* and *A. unsocalae*. Within this species group, the gill differs little in form, but the number of gill pleats in males varies considerably from 14 pleats in *A. pugetica* to 4 pleats in *A. eschrichtii*. The number of pleats seems to be independent of species size. Pleat number did vary with maturity. Thus, the pleat numbers shown in Figs. 19-20 cannot be regarded as diagnostic since terminal male instar specimens were not always available.

From this study, it was concluded that the "dendritic" gill is plesiomorphic and the "pleated" gill is apomorphic. The two sources of evidence for this conclusion are: 1) both types of gills show a reduction in the size and number of pleats in the development of the female, while the pelagic male stage, which is usually considered conservative, retains the juvenile gill form; 2) the "dendritic" species group is characterized as plesiomorphic on the basis of other characters (see Table 2 and Fig. 21). However, this inference should be re-evaluated when the gills of a broader representation of *Ampelisca* are known. Further insight will be gained by study of the gills of

related genera (*Byblis*, *Haploops*) and related superfamilies (Dexaminoidea). Since the pattern of sexual dimorphism in *Ampelisca* is for a flatter, less space-consuming gill in mature females, it suggests that this is an adaptation to allow larger broods without a corresponding increase in body size. However, this suggestion should be re-evaluated when more is known of the activity patterns and respiratory physiology of brooding females.

In an effort to elucidate subgeneric groupings among the species of *Ampelisca* from our study area, a cluster analysis was performed using the 24 characters listed in Table 1. Each character was defined in such a way that every species could be classified into one of 2 to 4 character states depending on the character. This coding process resulted in the data matrix of species versus characters shown in Table 2. Using the data matrix, a similarity matrix was generated using the simple matching coefficient (see Sneath and Sokal 1973, p. 132). The similarity matrix gives an index of morphological resemblance for each possible species pair. From the similarity





Figure 20. Representative coxal gills of *Ampelisca brevisimulata*, ♀ 7 mm, ov, ♂ 6 mm, subadult; *Ampelisca careyi* ♀ 8 mm, ov, ♂ 7 mm, subadult; *Ampelisca cristata* ♀ 17 mm, ov, ♂ 12 mm, subadult; *Ampelisca eschrichti* ♀ 20 mm, ov, ♂ 12 mm, subadult; *Ampelisca hessleri* ♀ 7 mm ov, ♂ 6 mm, subadult; *Ampelisca milleri* ♀ 6 mm, ov, ♂ 6 mm, adult; *Ampelisca pugetica* ♀ 10 mm, ov, ♂ 7 mm, subadult; *Ampelisca unsocalae* ♀ 8 mm, ov, ♂ 7 mm, subadult.

matrix, a phenogram was generated using the method of complete linkage clustering (see Sneath and Sokal 1973, p. 222). Although these techniques are among the simplest methods of classification analysis, they seemed sufficient for the level of discrimination desired and had the advantage of being easily performed without the use of a large computer.

In analysing the phenogram (Fig. 21), it should be kept in mind that the relationships shown in it reflect only the morphological resemblance of

these species and inference of phyletic relationships from it should be done with caution. The interpretation of a cluster analysis can be complicated by two factors not considered in the methodology: convergence and negative matches. Either of these factors can give two species a higher phenetic resemblance than appropriate for their phyletic relationship. However, despite these weaknesses in the methodology, some useful insights may be gained from a careful examination of the phenogram.

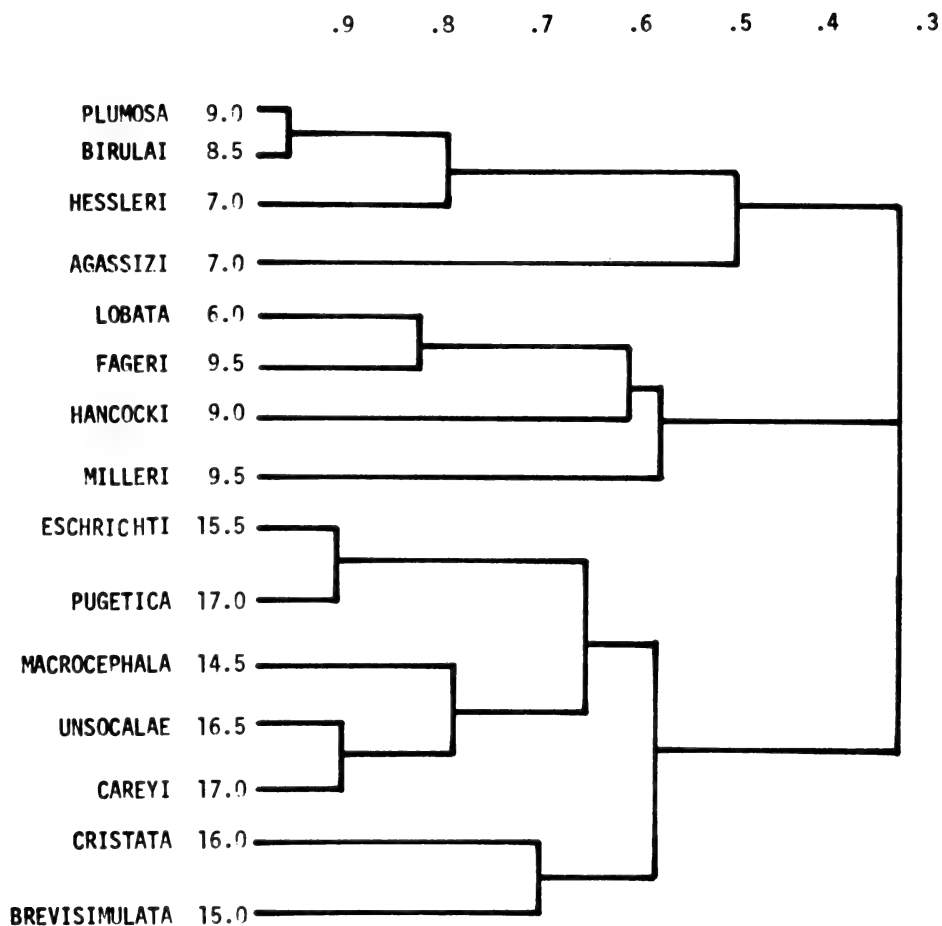


Figure 21. Phenogram showing morphological similarity of species of *Ampelisca* from Northeast Pacific region. Number beside each species is index of apomorphy. Scale across the top is the measure of similarity.

As a further aid in this analysis, each of the character states was designated as plesiomorphic (0), intermediate (.5) or apomorphic (1). Using these rankings, an index of apomorphy was calculated for each species (see Table 2). A species which was advanced in all characters would have an index of 24; whereas a species which was primitive in all characters would have an index of zero. Although this technique is rather subjective and the scoring of certain characters was questionable, the general trends shown by this method seem reasonable. The index for each species is listed on its line in the phenogram (Fig. 21).

The phenogram shows 3 distinct clusters of species: 1) *A. plumosa*, *A. birulai*, *A. hessleri*, and *A. agassizi*; 2) *A. lobata*, *A. fageri*, *A. hancocki* and *A. milleri*; 3) *A. eschrichti*, *A. pugetica*, *A. macrocephala*, *A. unsocalae*, *A. careyi*, *A. cristata* and *A. brevisimulata*. The first of these clusters contains 4 species which have very similar urosomal carinas and telsons. Three of the species (*A. plumosa*, *A. birulai*, and *A. hessleri*) are so similar in their morphologies that any suggestion of convergence can be dismissed reasonably. The relationship of *A. agassizi* to the other three species must be rather distant since they differ in so many characters (see Table 2) including the

structure of their gills, presence of coxal teeth, shape of basal lobe of pereopod 7, presence of comb spines on pereopods 5-6, relative lengths of mandibular palp segments, and structure of uropod 3. All four of the species in the *A. plumosa* cluster are relatively plesiomorphic with indices between 7 and 9.

The second cluster contains a rather anomalous group of plesiomorphic species which probably have little phyletic relationship. *A. fageri* and *A. lobata* share enough characters in the structure of their gills, mandibular palp, urosomal carina, uropod 3, and telson to indicate a fairly close phyletic relationship despite the large differences in their pereopod 7. The addition of *A. hancocki* and *A. milleri* to this pair seems artificial despite the near equivalence of their apomorphic indices. Their similarity is mainly due to their generalized structure which results in negative matches (see Table 2) and perhaps some convergence due to their small size. In any case, the differences in the mouthparts, pereopod 7, and telson seem sufficient to rule out any close relationship. *A. milleri* seems distinct from other North Pacific species, and its closest relatives are North Atlantic species such as *A. abdita* Mills 1963, and *A. vadorum* Mills 1964, which are extremely similar in their morphology (Mills 1965). *A. hancocki* is difficult to group. It is clearly closely related to *A. shoemakeri* described by Barnard (1954a) from the Pacific coast of central America. The presence of a tooth on pleon sideplate 3 and the shape of the urosomal carina suggest that it may be distantly related to the more apomorphic species in cluster 3, but it clearly has no close relatives in the British Columbia region.

The third cluster contains a group of apomorphic species all of which have a tooth on pleon sideplate 3, an apical spine on uropod 2, elongated segment 5 on gnathopod 2, comb spines on pereopods 5-6, and lanceolate third uropod. The three subgroupings within this cluster also seem to reflect probable phyletic relationships. *A. pugetica* and *A. eschrichti* both have an elongated uropod 2, and an anterior notch in segment 5 of pereopod 7. This combina-

tion of characters is so distinctive as to suggest a close phyletic relationship. *A. coeca* Holmes 1908, a bathyal species off California, is also clearly related to this species pair. *A. macrocephala*, *A. careyi* and *A. unsocalae* were previously considered one species and are clearly closely related. *A. cristata* and *A. brevisimulata* have similarities in their head shapes, coxal teeth, and pereopod 7 which suggest some degree of phyletic relationship. However, *A. brevisimulata* is much more similar to the North Atlantic species *A. verilli* Mills 1967 and *A. holmesi* Pearce 1908, and *A. cristata* is a closer relative of the tropical Pacific species *A. cristoides* Barnard 1954a.

Although the cluster analysis has been useful in pointing out possible phyletic relationships among the Northeast Pacific *Ampelisca*, it has also underlined the difficulty in trying to subdivide this large genus. Almost any of the twenty-four characters used in the analysis would give a unique set of clusters of the 15 species if used alone. This mosaic pattern of morphologies found in *Ampelisca* suggests a high degree of convergence in the group. It seems inadvisable to attempt any formal subdivisions of the genus until the morphologies of the world fauna are better documented, and even more importantly, a better understanding of their functional morphology is achieved.

The zoogeography of the 14 species of *Ampelisca* found in the Northeast Pacific region is summarized in Table 3. Three of the species (*A. birulai*, *A. eschrichti* and *A. macrocephala*) are arctic forms not found south of the Bering Sea. Nine species (*A. agassizi*, *A. brevisimulata*, *A. careyi*, *A. cristata*, *A. fageri*, *A. hancocki*, *A. lobata*, *A. pugetica* and *A. unsocalae*) have broad geographic ranges extending from the Queen Charlotte Islands to Mexico. This pattern would suggest that their habitat requirements and ecological tolerances must be relatively broad, but it also reflects the continuity of the cold temperate subtidal sand habitat along the Pacific coast of North America. The new species *A. hessleri* has been found only in northern British Columbia waters to date. Two species (*A. milleri* and *A. plumosa*) are not known north of central California.

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**Abbreviations For Figures**

Legend for all figures

Hd	head	UL	upper lip
Gn	gnathopod	LL	lower lip
P	peraeopod	Md	mandible
Cx	coxal plate	Lft	left
U	uropod	Rt	right
T	telson	Mx	maxilla
		Mxpd	maxilliped

**Table 1. List of Characters used in Cluster Analysis**

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1. Relative length of antenna 1 to peduncle of antenna 2 shorter (+), equal (0), longer (-)	12. Length of segment 6 of peraeopod 7 elongated (+), normal (-)
2. Shape of lower head margin concave (+), straight (0), convex (-)	13. Relative length of segment 3 to segment 4 on peraeopod 7 longer (+), subequal (-)
3. Number of coxal teeth 0, 1, 2, 3	14. Pleon sideplate 2 with tooth (+), without tooth (-)
4. Relative length of mandibular palp segment 3 to segment 2 > .75 (-), < .75 (+)	15. Pleon sideplate 3 with acute tooth (+), without tooth (-)
5. Mandibular palp segment 2 inflated (+), not inflated (-)	16. Gills pleated (+), dendritic (-)
6. Length of palm of gnathopod 1 elongate (0), simple (-), short (+)	17. Urosomal carina lamellar (+), massive (0), absent or reduced (-)
7. Relative length of segment 5 to segment 6 on gnathopod 2 ≥ .50 (+), < .50 (-)	18. Uropod 1 with outer ramus spinulose (+), unarmed (-)
8. Setation on posterior margin of segment 4 of peraeopod 3 entire (-), $\frac{1}{2}$ (0), $\frac{1}{3}$ (+)	19. Uropod 1 reaching end of uropod 2 (-), only reaching halfway along rami (+)
9. Comb spines on posterior margin of segment of peraeopods 5-6 well developed (+), reduced (0), absent (-)	20. Outer ramus of uropod 2 with apical spine (+), without apical spine (-)
10. Notch on anterior surface of segment 5 of peraeopod 7 present (+), absent (-)	21. Rami of uropod 3 long and lanceolate (-), short and flattened (+)
11. Shape of basal lobe of peraeopod 7 D shaped (-), "triangular" (+)	22. Apex of telson lobes notched (+), narrowed (0), blunt (-)
	23. Relative length of peduncular segment 2 to segment 1 of antenna 1 > 2X(+), < 2X (-)
	24. Dorsal spines of telson scattered (+), central rows (0), along cleft (-)

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Table 2. Data matrix of species vs. characters. Left entry is character state as defined in Table 1. Right entry indicates degree of apomorphy.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Ampelisca agassizi</i>	+1	0/.5	0/0	-0	-0	-0	-0	-0	+1	-0	+1	+1	-0	-0	-0	+1	0/.5	+1	-0	-0	-0	-0	+1	-0
<i>Ampelisca lobata</i>	-0	-0	3/1	-0	-0	0/.5	-0	+1	+1	-0	+1	-0	-0	-0	-0	-0	-0	-0	-0	-0	-0	+1	-0	0/.5
<i>Ampelisca fageri</i>	0/.5	-0	3/1	-0	-0	0/.5	-0	+1	+1	+1	+1	+1	-0	-0	-0	-0	-0	+1	-0	-0	-0	+1	-0	0/.5
<i>Ampelisca plumosa</i>	0/.5	-0	3/1	+1	-0	+1	+1	-0	-0	-0	-0	-0	-0	-0	-0	+1	0/.5	+1	-0	+1	+1	-0	-0	-0
<i>Ampelisca birulai</i>	0/.5	0/.5	3/1	+1	-0	+1	-0	-0	-0	-0	-0	-0	-0	-0	-0	+1	0/.5	+1	-0	+1	+1	-0	-0	-0
<i>Ampelisca hessleri</i>	-0	-0	3/1	+1	-0	0/.5	-0	+1	-0	-0	-0	-0	-0	-0	-0	+1	0/.5	+1	-0	-0	+1	-0	-0	-0
<i>Ampelisca brevisimulata</i>	+1	+1	1/.5	+1	-0	0/.5	+1	+1	+1	-0	+1	-0	-0	+1	+1	+1	0/.5	-0	-0	+1	-0	0/.5	+1	+1
<i>Ampelisca cristata</i>	+1	+1	1/.5	+1	-0	0/.5	+1	0/.5	+1	-0	+1	+1	-0	+1	+1	+1	+1	+1	-0	+1	-0	+1	-0	0/.5
<i>Ampelisca eschrichti</i>	-0	-0	2/.5	+1	-0	0/.5	+1	0/.5	+1	+1	+1	+1	-0	-0	+1	+1	0/.5	+1	+1	+1	-0	+1	+1	0/.5
<i>Ampelisca pugetica</i>	+1	-0	2/.5	+1	-0	0/.5	+1	+1	+1	+1	+1	+1	-0	-0	+1	+1	0/.5	+1	+1	+1	-0	+1	+1	0/.5
<i>Ampelisca hancocki</i>	+1	-0	3/1	+1	-0	0/.5	-0	0/.5	0/.5	-0	+1	-0	-0	-0	+1	-0	0/.5	+1	-0	-0	-0	+1	-0	-0
<i>Ampelisca macrocephala</i>	+1	-0	2/.5	+1	-0	+1	+1	+1	+1	-0	+1	+1	-0	-0	+1	+1	0/.5	+1	-0	+1	-0	+1	-0	0/.5
<i>Ampelisca careyi</i>	0/.5	+1	3/1	+1	-0	+1	+1	+1	+1	-0	+1	+1	-0	-0	+1	+1	0/.5	+1	-0	+1	-0	+1	+1	+1
<i>Ampelisca unsocatae</i>	+1	-0	3/1	+1	-0	+1	+1	+1	+1	-0	+1	+1	-0	-0	+1	+1	0/.5	+1	-0	+1	-0	+1	+1	+1
<i>Ampelisca milleri</i>	-0	-0	3/1	+1	+1	0/.5	-0	+1	0/.5	-0	+1	-0	+1	-0	-0	+1	-0	-0	-0	-0	-0	+1	-0	0/.5



**Table 3. Geographical distribution of Northeast Pacific *Ampelisca***

Species	Arctic Ocean & Beaufort Sea	Northern Bering Sea	Prince William Sound	Cross Sd. to Dixon Entrance & Queen Charlotte Islands	Northern B.C. & Northern Vancouver Island	Central B.C. & Southern Vancouver Island	Washington & Oregon	California & Mexico
<i>Ampelisca</i> <i>birulai</i>	X	X						
<i>Ampelisca</i> <i>macrocephala</i>	X	X						
<i>Ampelisca</i> <i>eschrichti</i>	X	X						
<i>Ampelisca</i> <i>pugetica</i>			X	X	X	X	X	X
<i>Ampelisca</i> <i>agassizi</i>				X	X	X	X	X
<i>Ampelisca</i> <i>careyi</i>				X	X	X	X	X
<i>Ampelisca</i> <i>cristata</i>				X	X	X	X	X
<i>Ampelisca</i> <i>brevisimulata</i>				X	X	X	X	X
<i>Ampelisca</i> <i>lobata</i>				X	X	X	?	X
<i>Ampelisca</i> <i>hessleri</i>				X	X			
<i>Ampelisca</i> <i>unsocalae</i>				X	X	X	X	X
<i>Ampelisca</i> <i>hancocki</i>					X	X	X	X
<i>Ampelisca</i> <i>fageri</i>						X	?	X
<i>Ampelisca</i> <i>milleri</i>								X
<i>Ampelisca</i> <i>plumosa</i>								X



# The Amphipod Superfamily Corophioidea in the Northeastern Pacific Region. Family Ampithoidae: Systematics and Distributional Ecology

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## ABSTRACT

The gammaridean family Ampithoidae of the boreal eastern Pacific coastal region (Alaska to Pt. Conception, California) is examined on a taxonomic, biogeographical and ecological basis. Keyed and described are fifteen species within the genera *Cymadusa* Savigny, *Ampithoe* (Leach, sens. str.) and *Peramphithoe* n.gen. This latter genus is erected for all species of *Ampithoe* bearing a transverse first gnathopod. *Ampithoe dalli* Shoemaker is reinstated as a species distinct from *A. simulans* Alderman. *Ampithoe sectimanus* n. sp., earlier confused as a variant of *A. pollex* Kunkel and *A. simulans* Alderman, is recognized as a distinct new species. The taxonomic status of *Peramphithoe mea* (Gurjanova), *P. tea* (Barnard), *P. plea* (Barnard) and *P. annenkovae* (Gurjanova) is clarified. For comparison, two anti-boreal eastern Pacific species, *Peramphithoe lessoniophila* n.sp. and *P. femorata* (Krøyer) are described. Thirteen of the fifteen North Pacific species are endemic to the boreal region and eight of these are restricted to the North American coast. Greatest diversity occurs on the central and Vancouver Island coasts (12 species) of British Columbia, pointing to this region as being the centre of distribution in the North-eastern Pacific.

## RÉSUMÉ

La famille de gammare Ampithoidae de la partie septentrionale de la côte orientale du Pacifique (de l'Alaska à la Californie — Point Conception) a fait l'objet d'une étude taxinomique, biogéographique et écologique. L'auteur fournit des clés et des descriptions de quinze espèces des genres *Cymadusa* Savigny, *Ampithoe* (Leach, sens. str.) et *Peramphithoe* n. gen. Ce dernier regroupe toutes les espèces d'*Ampithoe* qui ont un premier gnathopode transversal. *Ampithoe dalli* Shoemaker reprend le rang d'espèce, distincte d'*A. simulans* Alderman. *Ampithoe sectimanus* n. sp. antérieurement considérée comme une variante d'*A. pollex* Kunkel et d'*A. simulans* Alderman est maintenant reconnue comme une nouvelle espèce distincte. On fournit des éclaircissements sur le statut taxinomique de *Peramphithoe mea* (Gurjanova), *P. tea* (Barnard), *P. plea* (Barnard) et *P. annenkovae* (Gurjanova). A des fins de comparaison, la description de deux espèces anti-boréales, *Peramphithoe lessoniophila* n. sp. et *P. femorata* (Krøyer), apparaît dans ce travail. Parmi les espèces du Pacifique-nord, treize sur un total de quinze sont endémiques à la région boréale, tandis que huit d'entre elles sont restreintes à la côte de l'Amérique du Nord. La diversité la plus grande se rencontre en Colombie-britannique au centre de la côte et sur la côte de l'île de Vancouver, ce qui indique que cette région est le centre de la distribution dans le nord-est du Pacifique.

## Introduction

Members of the corophioidean family Ampithoidae inhabit self-constructed tubes in coastal marine algae. The family was first described by Stebbing (1888), individuals being distinctive in the incision of the outer lobes of the lower lip and the possession of shortened pad-like rami on the third uropod, the outer ramus of which bears one or two large reverted uncini.

The Ampithoidae is a primarily warm water family but species extend into the boreal regions of both the Atlantic and Pacific. This paper examines the Ampithoidae of the boreal and anti-boreal eastern Pacific. To date, the boreal Pacific Ampithoidae has been studied in California and Oregon by Barnard (1954, 1964, 1965, 1969b, 1970), on the Pacific coast of the USSR by

Gurjanova (1938, 1955) and Kudryashov (1979), and in Japan by Nagata (1960). Only 2 of the 11 known genera have boreal representatives (*Cymadusa* and *Ampithoe*). The intent of this study is to extend our knowledge of the boreal northeastern Ampithoidae from the southernmost limits of the region (Point Conception, California) to the northernmost limits in Alaska. In addition, information on a new anti-boreal species from South America is given.

The specimens from which information was compiled were collected mainly by National Museum survey expeditions. Station data for the expeditions of 1955 (Vancouver Island and Georgia Strait, B.C.), 1957 (Queen Charlotte Islands, B.C.), 1959 (northern Vancouver Island), 1961 (southern Alaska coast) and 1964 (northern and central British Columbia coast) are published in Bousfield (1957 and 1963), Bousfield and McAllister (1962), and Bousfield (1968), respectively. Station data for 1966 (Washington and Oregon), 1970, 1975 and 1977 (Vancouver Island and southern British Columbia mainland coast) and 1980 (southern Alaska coast) are presented in Bousfield and Jarrett (1981).

In order to facilitate identification, the keys and descriptions are constructed with sex and age independent characters, except where stated. Mature males are recognizable by their relatively large size for the species, enlarged and usually differentiated second gnathopod, and by the presence of paired penial papillae on the sternum of pereopod 7. Mature females are recognizable by their relatively large size and the presence of setose brood plates attached to the inner margin of coxae 2-5, below the sternum. Immature specimens are recognizable by their relatively small size, lack of brood plates and undifferentiated second gnathopod. Terminology of the appendages is by vertical orientation in relation to the body.

## SYSTEMATIC SECTION

### Family Ampithoidae Stebbing 1888<sup>1</sup>

Ampithoidae Stebbing, 1906, p. 631; J.L. Barnard, 1969a, p. 141-143, fig. 61; Bousfield, 1982, p. 285.

Ampithoidae Stebbing, 1899, p. 211

*Diagnosis:* Body smooth, little compressed. Pair of short setae on the dorsum of urosomites

1 and 2. Head, rostrum lacking, anterior lobe short and blunt, inferior antennal sinus shallow; eyes lateral, rounded, medium to small. Antennae medium to large. Antenna 1 peduncular segment 3 short, accessory flagellum short, vestigial or lacking. Antenna 2 peduncle strong.

Buccal mass directed below the head. Upper lip rounded below. Mandible, molar strong, palp slender or lacking. Left lacinia mobilis with 5 or more cusps. Lower lip, outer lobes with characteristic medial notch or emargination. Maxilla 1, inner plate small, outer plate with 10 (rarely less or more) apical spine-teeth. Maxilla 2, plates apically and medially setose, outer plate somewhat broadened. Maxilliped plates large, palp slender and dactylate.

Coxae 1-4 overlapping, deep, smooth or lightly setose below. Gnathopods usually strongly subchelate, 2 larger and sexually dimorphic. Pereopods 3 and 4 glandular, segment 2 expanded, distal segments short, dactyls with gland duct. Pereopods 5-7 dissimilar, distal segments may be reversed, segment 6 may expand and form a weak subchela with the dactyl; coxae 5, 6 and sometimes 7 strongly anterolobate, coxa 5 often as deep as coxa 4. Pleopods normal, retinacula more than 2.

Urosome segments separate, not shortened. Uropods 1 and 2 normally biramous. Uropod 3 biramous, rami very short, quadrate, inner setose, outer with 2 (occasionally 1) strong apical uncini. Telson short, apex usually with cusps. Brood plates with hook-tipped marginal setae (on pereopods 2-5). Gills laminar, plate-like, short pedunculate on pereopods 2-6.

Genera: *Amphithoides* Kossman 1880, *Amphitholina* Ruffo 1953, *Ampithoe* (Leach 1814), *Cymadusa* Savigny 1816, *Exampithoe* K.H. Barnard 1925, *Macropisthopous* K.H. Barnard 1916, *Paradusa* Ruffo 1969, *Peramphithoe* new genus, *Paragrubia* Chevreux 1901, *Pleonexes* Bate 1857, *Sunamphitoe* Bate 1857, *Pseudoamphithoides* Ortiz 1976

Animals are medium to large (5-35 mm) and

1. Some doubt exists concerning the orthography of the family name. Leach (1814) dedicated his genus to the Nereid 'Amphithoe' of Homer but erroneously transliterated the greek 'phi'. This has led to a confusion of spelling in subsequent publications. Although the authors agree with Ruffo (1969) and Myers (personal communication) that the philologically better form '*Amphithoe*' is preferable, it is felt that formal alteration by the International Commission on Zoological Nomenclature is first necessary.

spin isolated tubes (with the cement glands of peraeopods 3 and 4) on algae, eelgrass, stones and detritus, or in the case of *Amphitholina*, burrow into kelp stipes and holdfasts. All are

littoral and shallow-water marine or epibiontic, tropical, warm temperate to arctic-boreal in both northern and southern hemispheres.

# Key to Genera of the Ampithoidae of the Northeastern Pacific (Alaska to Northern California)

1. Antenna 1, accessory flagellum multi-segmented; palm of gnathopod 1 oblique; peduncular spinous process projecting distally below the rami of uropods 1 and 2. .... *Cymadusa* Savigny 1816 (p. 43)
- Antenna 1, accessory flagellum vestigial or absent; palm of gnathopod 1 transverse or oblique; peduncular spinous process well developed if palm transverse but absent if palm oblique ..... 2
2. Gnathopod 1, palm oblique, coxa 1 produced forward; peraeopods 3 and 4, segment 2 slender, less than  $\frac{3}{4}$  the width of its coxa; uropod 1 peduncular spinous process absent ..... *Amphithoe* Leach 1813-14 (sens. str.) (p. 45)
- Gnathopod 1, palm transverse, coxa 1 not produced forward; peraeopods 3 and 4, segment 2 strongly inflated, more than  $\frac{3}{4}$  the width of its coxa; uropod 1 peduncular spinous process present ..... *Peramphithoe* n. gen. (p. 60)

**Genus *Cymadusa*** Savigny 1816, Barnard 1969a  
*Cymadusa* Savigny, 1816  
*Grubia* Czerniavski, 1868  
*Acanthogrubia* Stout, 1912

*Type species: Cymadusa filosa* Savigny 1816 (Monotypy). See Chevreux and Fage, 1925 (as *Grubia hirsuta*), Shoemaker, 1935 (as *Grubia filosa*).

**Diagnosis:** Head lobe produced, inferior antennal sinus moderate. Antenna 1, accessory flagellum with  $1\frac{1}{2}$  to  $6\frac{1}{2}$  segments. Mandibular palp moderately strong. Maxilla 1 palp broad. Gnathopod 1, palm oblique, coxa 1 produced forward; gnathopod 2 subchelate, equal to or larger than 1. Peraeopods 3 and 4, segment 2 moderately inflated. Peraeopods 5-7, segment 6 not strongly widened apically, spines not restricted to the antero-distal region. Uropod 1, peduncle extended postero-distally into a long spinous process between the rami. Uropod 3, outer ramus with two hooked uncini. Telson with two small apical cusps. About 10 species, generally tropical to subtropical to cool temperate; littoral.

Northeastern Pacific species: *Cymadusa uncinata* (Stout 1912)

***Cymadusa uncinata*** (Stout 1912, Barnard 1969b) Figure 1.

*Acanthogrubia uncinata* Stout, 1912, p. 146, figs. 81-83

*Paragrubia uncinata* Shoemaker, 1941, p. 188; Hewatt, 1946, p. 199

*Cymadusa uncinata* J.L. Barnard 1965, p. 40, figs. 26-28

J.L. Barnard, 1969b, p. 86

**Material examined:** Alaska — Puffin Bay, Baranof Island: 12 immature specimens from Bousfield and McAllister 1961, stn. A171. British Columbia — Queen Charlotte Islands: 4 immature specimens from Bousfield 1957 stn. W8. Northern mainland: 48 specimens from Bousfield 1964 stns. H53, H65 and the collection of D.E. McAllister, 1965. Vancouver Island and southern mainland: 78 specimens from collections of Bousfield 1977 (stn. B6a), 1959 (stns. O5, O11, V4b, cat. 2606), 1955 (stns. P7, F2) and the collections of J.F.L. Hart 1934, 1939, 1941. Washington and Oregon — 54 specimens from Bousfield 1966 stns. W40, W42 and the collection of R.I. Smith, 1955. Smithsonian collections (USNM): Bousfield 1966 Stn. W40, 1 ♂, 1 ♀ subadult, 6 immatures.

**Distribution:** Baranof Island, Alaska (56°16'N, 134°48'W) to Laguna Beach, California (33°5'N, 117°8'W).

**Ecology:** Occurs amongst kelp and *Phyllospadix* in high salinity waters of exposed coasts at low tide, in the shallow subtidal or in tide pools. Females brood young May-August. Large overwintered females which have not developed setae on the brood plates can be found in the spring.

**Diagnosis:** Antenna 1 longer than 2, peduncular segments weakly setose, peduncle 1 bearing spines on postero-distal edge. Antenna 2 peduncle not

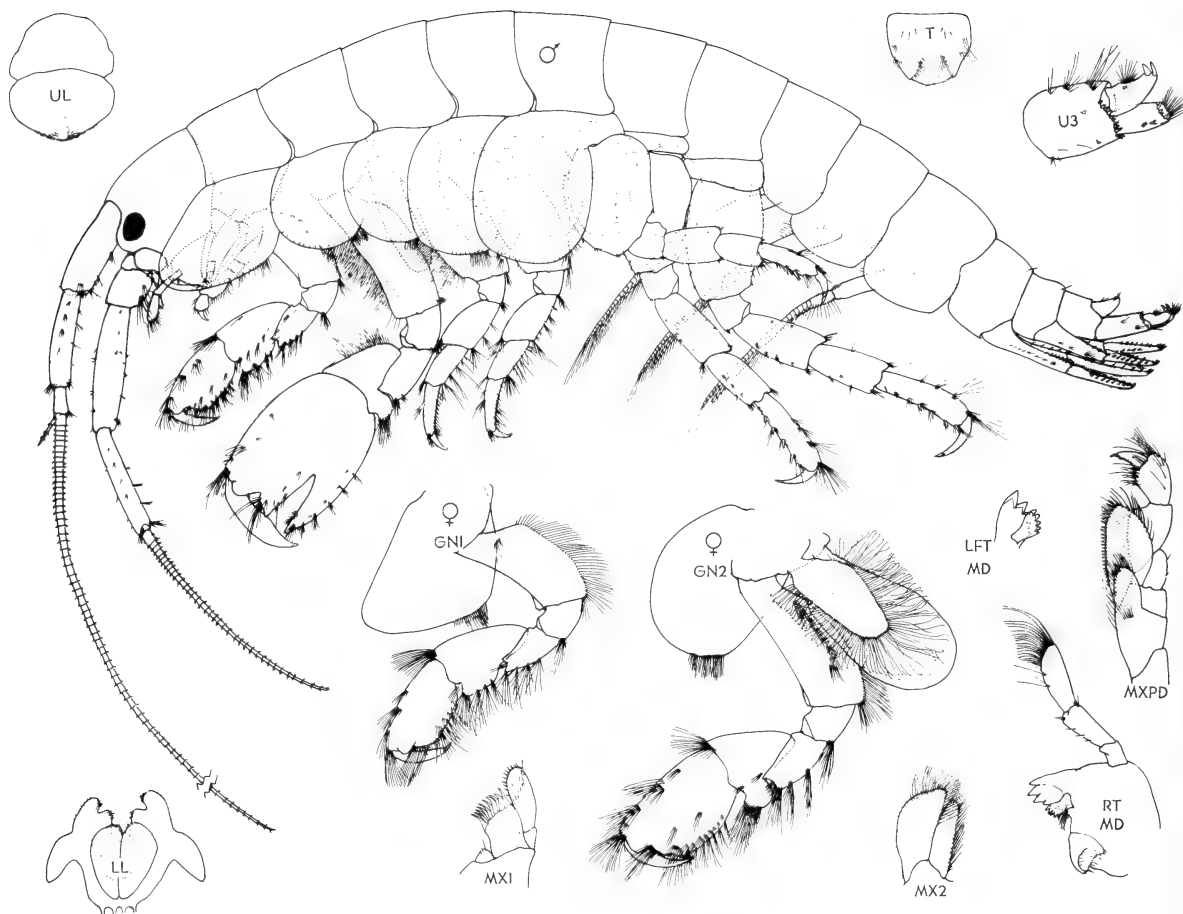


Figure 1. *Cymadusa uncinata* Stout ♂ 20.0 mm, Trial Island Point, Victoria, B.C. 18 May 1977; ♀ 23.0 mm, Shipwreck Point, Clallam County, Washington. 1 Aug. 1966

greatly stouter, flagellum equal in length to peduncle segments 4 and 5 together. Mandible, incisor with 9 teeth, 11 spines; lacinia mobilis with 6 teeth; palp segment 1 bare of setae, segment 2 setose on distal and inner margins, segment 3 longer than 2, distally rounded and strongly setose on distal and ventral margins. Lower lip outer lobes, apical somewhat longer than medial. Maxilla 1, inner plate with 3 setae; palp more than half the width of the outer plate, tipped with 10 spines and 8 setae. Maxilliped inner plate apically spinous; outer plate inner edge smooth, teeth smooth. Coxae 1-4 setose on lower margin. Coxa 1 produced forward, anterior edge straight; coxae 1 and 2 not shallower than 3-5. Gnathopod 1, both sexes, segment 2 with a small antero-distal lobe; segment 3 not lobed, segment 5 narrowed below into a shallow forward produced lobe; palm oblique, well defined, dactyl

serrated. Gnathopod 2 (♂) much larger than 1, segment 2 bearing long plumose setae on the anterior, medial and posterior margins; neither segment 2 nor 3 lobed; segment 5 bearing feathery setae on the upper margin; at about 15 mm body length, hand splitting into two large teeth, the ventral tooth much the longer, approaching half the length of the hand; dactyl slightly sinuous, projecting beyond the hand. Gnathopod 2 (♀) somewhat larger than gnathopod 1, lacking plumose setae or teeth as in the male. Peraeopod 3 similar to, though slightly longer than 4, segment 2 expanded, but less than the width of its body segment, segment 4 slightly less than half the width of segment 2; male peraeopod 3, anterior edge of segment 2 bearing plumose setae. Peraeopods 5-7, anterior edge of segment 2 spinous, segment 4 longer than 5, segment 6 bearing 5-7 groups of strong spines.

Epimeral plates, lower hind corners acute but not notched and lacking a lateral ridge. Pleopod outer rami slightly shorter than inner, bearing 5-6 anchor-shaped coupling hooks. Urosome 1 sternum setose. Uropods 1 and 2 bearing lateral tufts of setae on the peduncle and outer ramus, peduncular process well developed, outer ramus shorter than inner, spines small and abundant, 2-4 at tip. Uropod 2 reaching somewhat beyond 1. Uropod 3 long, peduncle bearing 2 central spines and 12 distal "crown" spines, inner ramus with 2 central and 5 distal spines, outer ramus with 1 central and two well developed hooked uncini. Telson with a row of 10-15 apical setae. Female brood plates relatively small, reaching not more than two-thirds the length of peraeopod segment 2. Body length at maturity: ♂ 15-35 mm, ♀ 20-35 mm. This is the largest species of *Cymadusa* and one of the largest amphipods on this coast.

*Remarks:* *Cymadusa uncinata* can be distinguished from the North Atlantic species *C. filosa* and *C. compta* by its much greater body size (up to 35 mm as opposed to 15 mm), the unequal sizes of gnathopods 1 and 2 and the deeply incised palm of gnathopod 2 (♂). *Cymadusa* most closely resembles *Ampithoe* (sens. str.) but differs mainly in the presence of a distinct accessory flagellum, long peduncular process of uropod 1 and more setose maxilla 1 plate (3-6 setae as opposed to 0-2 setae). These characteristics are considered plesiomorphic, and suggest that *Cymadusa* is ancestral to *Ampithoe*.

**Genus *Ampithoe*** (Leach 1813-14) emend. (sens. str.)

*Ampithoe* Leach, 1813-14, p. 403, 432; Stebbing, 1906, p. 631-632;

J.L. Barnard, 1969a, p. 143, 144, fig. 61

*Type species: Ampithoe rubricata* (Montagu 1808) (type by original designation).

Species contained in the genus *Ampithoe* have recently been found by the authors to be of three basic types. These differ on a significant basis in several prime morphological characters, hence justifying subdivision into the genera *Ampithoe* (sens. str.), *Peramphithoe* and *Pleonexes*. Details of this analysis are to be published separately. (Conlan, 1982).

*Diagnosis:* Head lobe produced, antennal sinus present. Antenna 1 accessory flagellum minute, one-segmented. Mandibular palp moderately weak to strong. Maxilla 1 palp relatively broad. Gnathopod 1, palm oblique, coxa 1 produced forward. Gnathopod 2 subchelate, equal to or larger than 1. Peraeopods 3 and 4, segment 2 moderately inflated. Peraeopods 5-7, segment 6 little distally expanded, spines usually not restricted to the antero-distal region. Uropod 1, peduncular process vestigial or absent. Uropod 3, outer ramus with two apical hooked spines or uncini. Telson with two small apical cusps. About 37 species, arctic-boreal to tropical, littoral.

Northeastern Pacific species: *Ampithoe valida* Smith 1873, *A. lacertosa* Bate 1858, *A. simulans* Alderman 1836, *A. volki* Gurjanova 1938, *A. dalli* Shoemaker 1938, *A. plumulosa* Shoemaker 1938, *A. rubricatoides* Shoemaker 1938, *A. kussakini* Gurjanova 1955, *A. sectimanus* n.sp.

#### Key to Species of *Ampithoe* of the Northeastern Pacific

1. Gnathopod 1, lower lobe of segment 5 broad, more than half the length of the full segment. Peraeopods 3 and 4 slender, segment 4 less than half the width of segment 2. Gnathopod 2 (♂), both segments 2 and 3 produced into a large anterodistal lobe ..... 2
- Gnathopod 1, lower lobe of segment 5 less than half the length of the full segment. Peraeopods 3 and 4 strong, segment 4 more than half the width of segment 2. Gnathopod 2 (♂), only segment 2 produced into an anterodistal lobe ..... 4
2. Antenna 2 with dense plumose setae on peduncle 5 and flagellum. Epimeron 3, hind margin evenly rounded. Gnathopod 1 (♂), segment 5 shorter than segment 6. Gnathopod 2 (♂), palm sinuous, slightly oblique ..... *Ampithoe plumulosa* Shoemaker 1938 (p. 50)
- Antenna 2 lacking dense plumose setae. Epimeron 3, hind margin slightly to strongly notched. Gnathopod 1 (♂), segment 5 longer than segment 6. Gnathopod 2 (♂), palm transverse ..... 3
3. Antenna 1 peduncle 1 setose but lacking ventral spines. Coxae 1-4 with a group of long setae on the lower hind margin. Epimeron 3, hind margin only faintly notched and lacking a lateral

- ridge. Gnathopod 1 (♂), front margins of segments 5 and 6 bearing long overhanging simple setae. Gnathopod 2 (♂), palm with a median quadrate tubercle, hind margin not produced ..... *Ampithoe valida* Smith 1873 (p. 49)
- Antenna 1 peduncle 1 setose and bearing one to several spines on the ventral margin. Coxae 1-4 lacking a group of long setae on the lower hind margin. Gnathopod 1 (♂), front margins of segments 5 and 6 bearing upright plumose setae. Epimeron 3, hind margin with a strong notch, from which radiates a lateral ridge. Gnathopod 2 (♂), palm sinuous, hind corner produced downwards with age, lacking median tubercle ..... *Ampithoe lacertosa* Bate 1858 (p. 47)
4. Antenna 1 subequal to antenna 2. Antenna 2, peduncle moderately to strongly setose; flagellum shorter than segments 4 and 5 together. Uropods 1 and 2, rami tipped by several spines. Coxae 1 and 2 (♂) same depth as coxae 3-5 ..... 5
- Antenna 1 shorter than antenna 2. Antenna 2, peduncle weakly setose; flagellum as long as segments 4 and 5 together. Uropods 1 and 2, rami tipped by a single heavy spine. Coxae 1 and 2 (♂) shallower than 3-5 ..... 8
5. Antennae 1 and 2, peduncles strongly setose; antenna 1 peduncle 1 without a posterodistal spine. Anterior margin of segment 2 of pereopods 3-5 strongly setose. Maxilliped outer plate teeth serrated. Gnathopod 2 (♂), palm strongly incised to form a pointed tooth ..... *Ampithoe sectimanus* n. sp. (p. 54)
- Antennae 1 and 2, peduncles not strongly setose; antenna 1 peduncle 1 with a spine on the posterodistal angle. Anterior margin of segment 2 of pereopods 3-5 bare. Maxilliped outer plate teeth smooth. Gnathopod 2 (♂), palm not strongly incised, defining tooth small and square or minute ..... 6
6. Mandibular palp, segment 3 distally pointed and oblique, setae apical; segment 2 with 1 setae. Gnathopod 2 (♂), segment 5 as long as deep; palm incised to form a square tooth at posterior corner ..... *Ampithoe volki* Gurjanova 1938 (p. 53)
- Mandibular palp segment 3 rounded, apically and laterally setose; segment 2 with more than 1 seta. Gnathopod 2 (♂), segment 5 longer than deep; palm oblique, small rounded tooth at posterior corner ..... *Ampithoe kussakini* Gurjanova 1955 (p. 52)
7. Antenna 2, peduncle 5 and flagellum with conspicuous groups of setae on hind margin. Uropod 1 strongly spinose, with about 15 spines on the outer margin of the peduncle and about 25 on the outer ramus. Uropod 3 peduncle with mid-dorsal spines in addition to the usual distal crown spines. Gnathopod 2 (♂), hand not greatly enlarged, less than twice the size of the hand of gnathopod 1, palmer teeth absent ..... *Ampithoe rubricatoides* Shoemaker 1938 (p. 56)
- Antenna 2 weakly setose. Uropod 1 with less than half as few spines on peduncle and rami. Uropod 3 with distal crown spines only. Gnathopod 2 (♂), hand greatly enlarged, more than twice the size of the hand of gnathopod 1, with a strong tooth at the hind corner of the palm and at the dactyl hinge ..... 8
8. Mandibular palp, terminal segment acutely oblique, distal margin demarcated by a definite angle from the inner margin and setose for about half the length. Gnathopod 1 (♂), developing (at about 8 mm size) plumose setae on segments 2-5. Gnathopod 2 (♂), palm barely concave, hind margin produced into a small tooth which in the full adult does not meet the dactyl ..... *Ampithoe dalli* Shoemaker 1938 (p. 56)
- Mandibular palp, distal margin of segment 3 very oblique, rounding smoothly into the inner margin and setose for nearly the full length. Gnathopod 1 (♂), developing (at about 12 mm size) plumose setae on segment 2 only. Gnathopod 2 (♂), palm strongly concave, hind margin produced into a long tooth which meets the dactyl ..... *Ampithoe simulans* Alderman 1936 (p. 58)



The northeastern Pacific species of *Ampithoe* may be clustered into three subgroups which, on further study, may warrant formal taxonomic recognition:

1. *A. lacertosa*, *A. valida*, *A. plumulosa*
2. *A. kussakini*, *A. volki*, *A. sectimanus*
3. *A. rubricatoides*, *A. dalli*, *A. simulans*.

Characteristics which order the species are: reduction in size of the antennal sinus, shortening of antenna 1 with concurrent strengthening of antenna 2, increasing obliqueness of mandibular palp segment 3, increasing roundness of the coxae, narrowing of the segment 5 lobe of gnathopod 1, increasing obliqueness and concavity of male gnathopod 2, increasing glandularity of pereopods 3 and 4, strengthening of the uropod 3 uncini, loss of the lateral ridge on the epimera, an overall deepening of the body and shallowing of the coxae. The functional significance of these morphological changes suggest a trend towards greater domicoly.

**Group of *Ampithoe lacertosa*, *A. valida*, *A. plumulosa***

Head, lateral lobe and antennal sinus prominent, eye medium. Antenna 1 equal to or longer than antenna 2, peduncle poorly setose. Antenna 2 very little stronger than antenna 1, flagellum equal to or shorter than peduncular segments 4 and 5 combined. Mandibular palp segment 3 apically blunt, distally setose. Coxa 1 anterior margin straight or slightly upcurved; coxae 1 and 2 (♂), shallower than 3-5; coxa 5 in both sexes, lower corners acutely rounded. Gnathopod 1, posterior lobe of segment 5 broad, more than half the length of the full segment and in the male, produced distally under segment 6. Gnathopod 2 (♂), both segments 2 and 3 produced into a prominent antero-distal lobe, palm transverse or slightly oblique. Pereopods 3 and 4 slender, segment 4 less than half as wide as segment 2. Pereopods 5-7 slender, spines weak. Uropods 1 and 2, rami ending in a group of 2-4 spines. Epimera 1-3 with a lateral ridge. Pleopods with 8-11 coupling hooks. Uropod 3 long, apical uncini of outer ramus weak.

The species trend phyletically in the increased shortening of antenna 1 relative to antenna 2, increasing obliqueness of mandibular palp segment 2 and increasing obliqueness of the male palm of gnathopod 2. *Ampithoe japonica* Stebbing 1888 and *A. cavimana* Sivaprakasam 1970, seem referable to this group.

***Ampithoe lacertosa* Bate 1858, Barnard 1965**

Figure 2.

*Ampithoe lacertosa* Bate 1858, p. 362; 1862, p. 236-237, pl. 41, fig. 5; Gurjanova, 1951, p. 895-897, fig. 622.

*Ampithoe lacertosa* Stebbing, 1906, p. 633-634; J.L. Barnard, 1954, p. 31-33, pls. 29-30; J.L. Barnard, 1965, p. 9-12, figs. 4, 5; Nagata, 1960, p. 175-176, pl. 16, figs. 95-96; Heller, 1968, p. 1-132; J.L. Barnard, 1969b, p. 83

*Ampithoe macrurus* Stephensen, 1944, p. 80-83, figs. 30-31

*Dexamine scitulus* Harford, 1877, p. 116

*Ampithoe scitulus* Holmes, 1904, p. 314-315, pl. 36, figs. 21-24

? *Ampithoe stimpsoni* Boeck, 1871, p. 14-15, fig. 5; Stebbing, 1906

*Material examined:* Alaska — Aleutian Islands: 1 immature specimen from Izembek Lagoon, Unimak Is., 1969, N.A. Powell collector. South-eastern Alaska: 123 specimens from Bousfield and McAllister 1961 stations, A3, A7, A18, A27, A48, A87, A91, A92, A96, A107, A115, A131, A139, A147, A151, A174, A175; 5 specimens from Bousfield 1980 stns., S8B1 and S23F1. British Columbia — Queen Charlotte Islands: 60 specimens from Bousfield 1957 stns., W3a, W4a, W14, H2, H2a, H8b, H9, H10, H11, E5, E9, E12, E14a, E14c, E24, E25. Northern mainland: 169 specimens from Bousfield 1964 stns., H1, H3, H8, H10, H23, H25, H26, H29, H30, H33, H47, H48, H50, H52, H56, H57, H65. Vancouver Island and southern mainland: 1336 specimens from the collections of Bousfield 1977, 1976, 1975, 1970, 1964, 1959, and 1955, and from the collections of C. Carl, K.E. Conlan, D.V. Ellis, J.F.L. Hart, D. Kittle, C.D. Levings, C. Lobban, R.J. Long, N.A. Powell.

Washington and Oregon — 77 specimens from Bousfield 1966 stns., W8, W10, W13, W30, W33, W42, W44, W47, W64 and 10 specimens from the collections of S. Helen, 1967 and N. McDaniel, 1977.

Smithsonian Collections (USNM): Bousfield 1975 stn. P16a, 1 ♂, 1 ♀.

*Distribution:* Aleutian Islands, Alaska (50°N, 163°W) to Magdalena Bay in Baja California (25°N, 112°W); Japan, south to Shizuoka prefecture (35°N, 138°E).

*Ecology:* Found amongst algae, eelgrass or woody debris, on mud, sand and gravel beaches, in tidepools or on wharf pilings at low water or

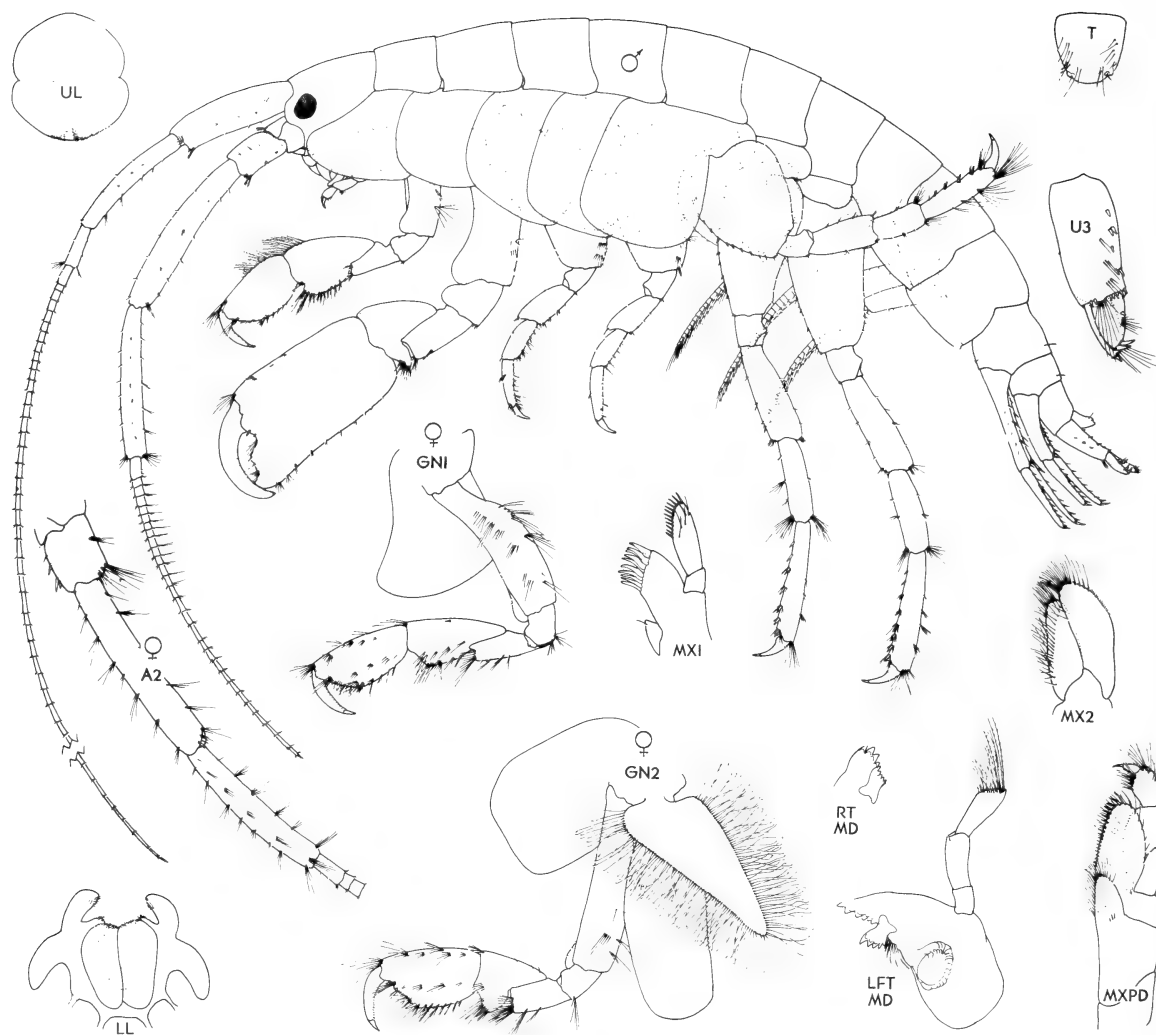


Figure 2. *Ampithoe lacertosa* Bate ♂ 21.5 mm; ♀ 30.0 mm, Friday Harbor, San Juan Is., Washington. April 1977

subtidally to about 10 m depth. It is equally abundant in high salinity exposed coastal waters and mesohaline shallow coastal waters but is rarely found in brackish water. Females are ovigerous from May to August.

**Diagnosis:** Antenna 1 longer than antenna 2, peduncle 1 with 1-4 posterior marginal spines (although absent in immatures). Antenna 2 peduncle not spinose, flagellum equal in length to peduncular segments 4 and 5 together. Mandibular palp segment 3 blunt, apically setose, 1 small seta on the distal corner of segment 2. Lower lip outer lobe, apical and medial lobes well separated, apical longer than medial.

Maxilla 1 inner plate with 1 seta, palp strong, with about 12 marginal spines. Maxilliped palp segment 1 lacking setae. Coxae 1-4 lacking long setae on lower margin. Gnathopod 1 both sexes, segment 6 slender, width less than half the length. Gnathopod 1 (♂), segment 5 longer than 6, margins of segments 5 and 6 developing a growth of plumose setae when body length is 12 mm or more. Gnathopod 2 (♂), segment 2 poorly setose, palm transverse, sinuous, lacking a median tubercle, hind edge produced downwards progressively with age to form a wide thumb. Male sternum of pereopod 7 lacking a median keel between the penes. Epimera 1-3 with strong

notch in hind corner (in immatures as well) from which radiates anteriorly a lateral ridge. Uropod 3 peduncle bearing dorsal spines along its length in addition to a crown of spines on the distal margin.

Body colour in life is orange to brown, heavily speckled. Distinctive white spot on the dorsum of each segment; some white spotting also on the coxae. Body length at maturity: Male 12-24 mm, female 10-23 mm. The male gnathopod 2 becomes transverse at as small a size as 7 mm but gnathopod 1 does not become plumose until the body is about 12 mm in length. A plot of the body length of 81 specimens against geographic distribution indicates a northward trend towards increased body length at maturity. The average size of maturity in Vancouver Island, southern B.C., Washington and Oregon was 16 mm ♂, 14 mm ♀, while in Alaska and northern B.C. the average was 17 mm ♂, 17 mm ♀.

*Remarks:* Heller (1968) described extensively the biology and development of this species.

*Ampithoe valida* Smith 1873

Figure 3.

*Ampithoe valida* Smith, 1873, p. 563; Paulmier, 1905, p. 164-165, fig. 34

*Ampithoe valida*, Stebbing, 1906, p. 635; Alderman, 1936, p. 68; J.L. Barnard, 1954, p. 34-35, pl. 31; Nagata, 1960, p. 176, pl. 16, figs. 97-98; J.L. Barnard, 1965, p. 34-36, figs. 22, 23; Bousfield, 1973, p. 180-181, pl. LV.1

*Ampithoe shimizuensis* Stephensen, 1944, p. 77-80, figs. 27-28

*Material examined:* British Columbia — Vancouver Island and southern mainland: 67 specimens from the collections of Bousfield 1976 (stns. B3, B11a, B13); 1975 (stns. P6a, P6b, P6c, P18a), 1970 (stns. P706, P709), 1959 (stn. N17), 1955 (stns. F1, F2a, F10, G11, G13, G22,

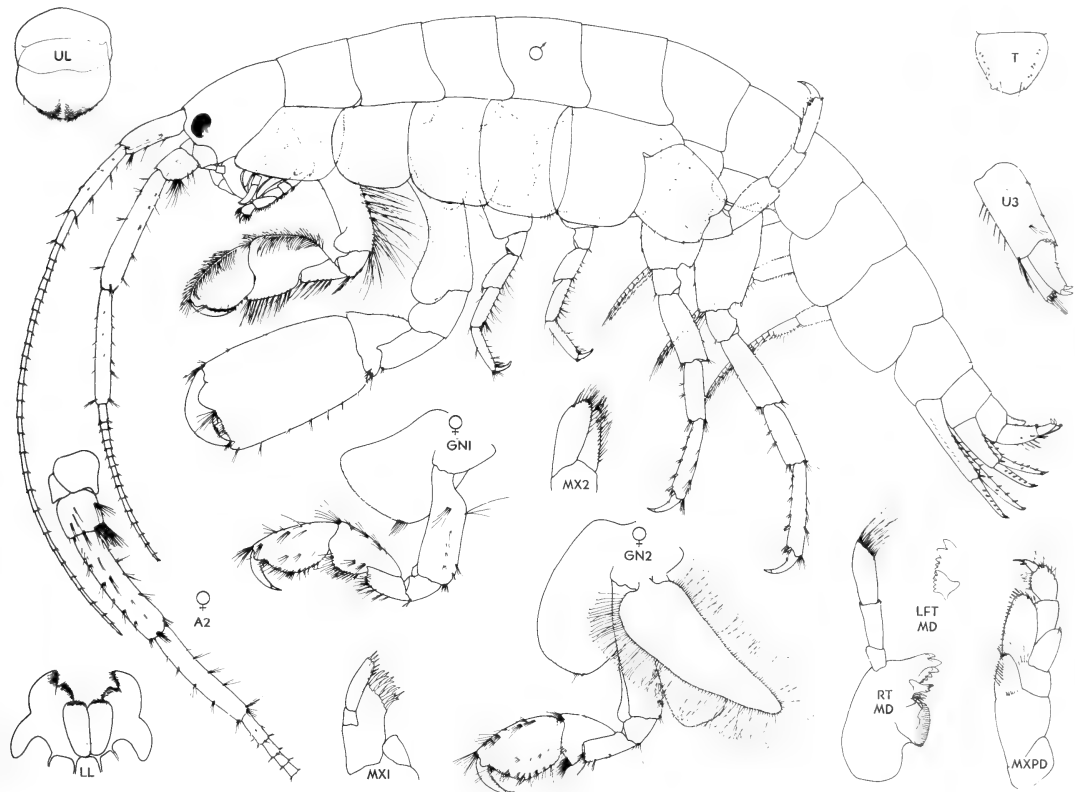


Figure 3. *Ampithoe valida* Smith ♂ 12.0 mm, Sarita Bay, Barkley Sound, Vancouver Is., B.C. 2 July 1977; ♀ 12.0 mm Brady's Beach, Barkley Sound, Vancouver Is., B.C. 31 July 1975

M1a, M2, M4, M5, M8, M10, M11). Four specimens also examined from the collections of M.A. Bousfield, K.E. Conlan, D.V. Ellis and R.J. Long.

Washington and Oregon — 12 specimens from Bousfield 1966 stns. W28, W47 and W64. Smithsonian collections (USNM): Bousfield 1975 stn. P6a, 2 ♂♂, 2 ♀♀.

*Distribution:* Pacific Ocean: British Columbia and Vancouver Island at 51° latitude south to Newport Bay, California (45°N, 124°W), ? Japan at Shizuoka Prefecture (35°N, 138°E). Atlantic Ocean: Piscataqua estuary, New Hampshire (43°N, 70°W) south to Chesapeake Bay, Virginia (37°N, 76°W).

*Ecology:* A warm temperate species occurring along sheltered coasts and estuaries, mainly in mesohaline to brackish waters. It builds tubes on algae and eelgrass on muddy, gravelly beaches in saltmarshes, tidepools and log fouling communities, at low water level to 30 m depth. Females brood from May to August. Immatures are brooded for about 2-5 weeks and grow about 1 mm/week, reaching maturity in about 6 weeks (Nicotri, 1980).

*Diagnosis:* Antenna 1 slightly longer than (♂) or equal to (♀) antenna 2; peduncle 1 setose but lacking posterior marginal spines. Antenna 2 peduncle not spinose, flagellum shorter than segments 4 and 5 together. Mandibular palp segment 3 obliquely truncate, apically setose, 1 small seta on the distal corner of segment 2. Lower lip, outer lobe, apical and medial lobes closely appressed, apical only slightly longer than medial. Maxilla 1 inner plate lacking setae, palp rather weak, with about 6 marginal spines. Maxilliped palp segment 1 setose. Coxae 1-4 bearing a group of long setae on the lower margin. Gnathopod 1, both sexes, segment 6 subcircular, width more than half the length. Gnathopod 1 (♂), segment 5 longer than 6, upper margins of segments 5 and 6 fringed with dense overhanging setae. Gnathopod 2 (♂), hind margin of segment 2 strongly setose, palm transverse, developing a median quadrate tubercle at about 6 mm body length, but not produced antero-distally with age. Male sternum 7 lacking a median keel between the penes. Epimera 1-3 with lateral ridge, hind margins rounded, with one short seta at hind corner. Uropod 3 lacking dorsal spines other than the usual marginal crown spines.

In life, body olive green to brown, and heavily

speckled. Body length at maturity: Male 6-12 mm, female 5-12.5 mm.

*Ampithoe plumulosa* Shoemaker 1938

Figure 4. (after Shoemaker 1938)

*Ampithoe plumulosa* Shoemaker 1938, p. 16-19, fig. 1; 1942, p. 39; J.L. Barnard, 1959, p. 37; 1964, p. 111; 1965, p. 20, figs. 11, 12; 1969b, p. 84.

*Material examined:* No material available. Information compiled from Shoemaker (1938), Barnard (1964, 1965 and 1969b).

*Distribution:* Patos Island, British Columbia (48°48.7'N) to Salinas, Ecuador; Galapagos Island (0°N, 90°W).

*Ecology:* A warm water species found amongst algae and *Phyllospadix* on pilings, floating docks, mud beaches and in tidepools, intertidal to a depth of about 15 m.

*Diagnosis:* Antenna 1 slightly longer than 2, peduncle 1 with up to 6 ventral spines. Antenna 2 peduncle may bear a few dorsal spines on segment 3 (but see remarks below); peduncular segment 5 and flagellum of antenna 2 clothed in abundant plumose setae. Mandibular palp segment 3 obliquely truncate, apically and somewhat laterally setose, 3 long setae on the margin of segment 2. Lower lip outer lobe, apical and medial lobes well separated, apical longer than medial. Maxilla 1 inner plate with 4 setae, palp strong, with about 8 marginal spines. Maxilliped palp segment 1 setose. Coxae 1-4 lacking long setae on hind margin. Gnathopod 1, both sexes, segment 6 slender, width less than half the length. Gnathopod 1, male, segment 5 shorter than 6, upper margins of segments 5 and 6 not strongly setose. Gnathopod 2, male, hind margin of segment 2 not strongly setose, palm slightly oblique, sinuous, forming a low flat tooth with age. Male sternum 7 bearing between the penes a median, lamellar, oval keel armed with marginal teeth which extends about  $\frac{2}{3}$  the depth of the penes (see Shoemaker, 1938). Epimera 1-3 hind margins evenly rounded, lateral ridge on each (but see remarks below). Uropod 3 lacking dorsal spines other than the usual marginal crown spines. Body length at maturity: Male 13-16 mm, female 12 mm.

*Remarks:* The illustrations of *Ampithoe plumulosa* collected in Bahia de San Quintin by Barnard (1965) differ in some respects from Shoemaker's type collected on Catalina Island, California. Antenna 2: type male (16 mm) lacks

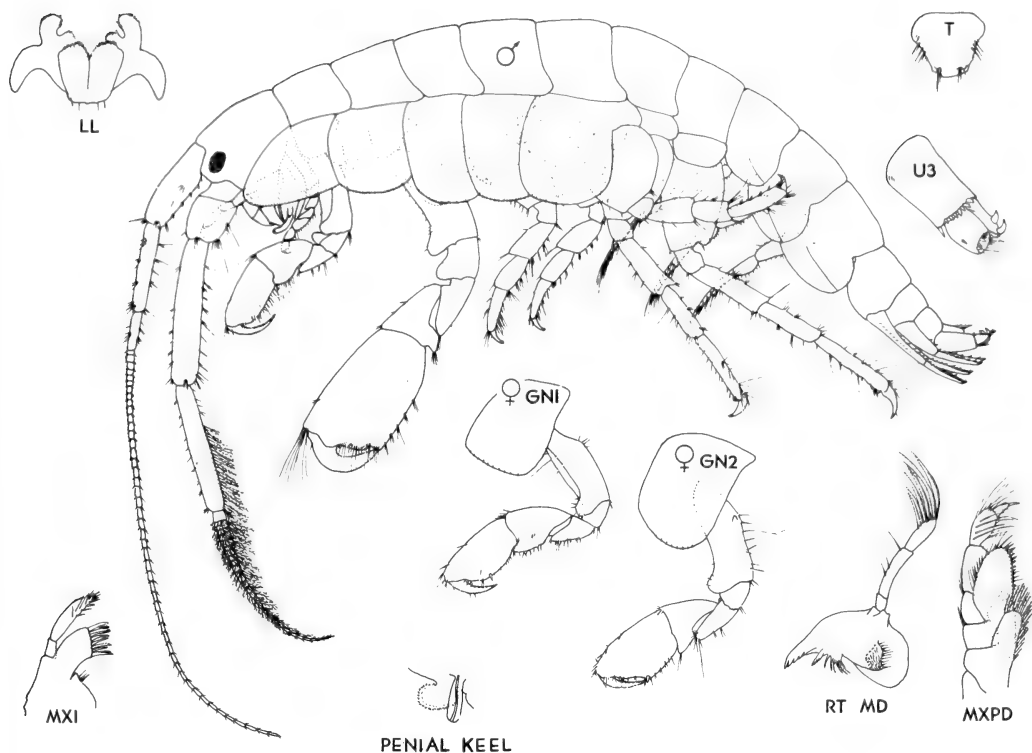


Figure 4. *Ampithoe plumulosa* Shoemaker ♂ 16 mm, La Jolla, California. 20 Sept. 1918. Reconstructed from Shoemaker, 1938

spines on peduncle, while the male (13 mm) figured by Barnard bears 4 anterior marginal spines on peduncle segment 3. Epimera 1 and 2: lateral ridges are illustrated on Shoemaker's type, yet are stated by Barnard to be absent. Only three specimens have been documented (by Shoemaker, 1938) for the Pacific coast north of lower California.

**Group of *Ampithoe kussakini*, *A. volki*, *A. sectimanus***

Head, lateral lobe and antennal sinus prominent; eye small. Antennae 1 and 2 subequal, peduncle moderately to strongly setose. Antenna 2 somewhat heavier than antenna 1, flagellum shorter than peduncular segments 4 and 5 together. Mandibular palp segment 3 oblique, laterally setose. Coxa 1 produced forward, anteriorly upturned; coxae 1 and 2 (♂) as deep as 3-5; coxa 5 in both sexes, lower corners evenly rounded. Gnathopod 1, lower lobe of segment 5

narrow, less than half the length of the full segment and not produced under segment 6. Gnathopod 2 (♂), segment 3 not produced into an anterior lobe, palm oblique and weakly concave, developing a small to long projection at the hind corner. Peraeopods 3 and 4 normal, segment 4 more than half as wide as segment 2. Peraeopods 5-7 normal, spines strong. Epimera 1-3 with or without a lateral ridge. Pleopods with 6-9 coupling hooks. Uropods 1 and 2, rami tipped by a group of 2-4 spines. Uropod 3 long, uncini of outer ramus moderately strong.

The species sequentially trend to reduction of the antennal sinus, increasing strength of setation on antennae, peraeopods and uropod 1, the increasing obliqueness in mandibular palp segment 1, increasing degree of incision of the male gnathopod 2 palm and a loss of the lateral ridge of epimeron 3.

Other species exhibiting affinities with this group: *Ampithoe djakonovi* Gurjanova 1938,

*Ampithoe longimana* Smith 1873, *Ampithoe platycera* Sivaprakasam 1970, *Ampithoe ramondi* Audouin 1826, *Ampithoe zachsi* Gurjanova 1938.

***Ampithoe kussakini* Gurjanova 1955**

Figure 5.

*Ampithoe kussakini* Gurjanova 1955, p. 215-217, figs. 22, 23

**Material examined:** Alaska — Aleutian Islands: 63 specimens from the collections of C.E. O'Clair, 1970 and 1972 and N.A. Powell 1969. South-eastern Alaska: 144 specimens from Bousfield and McAllister 1961 stns. A7, A19, A20, A25, A27, A30, A43, A68, A70, A71, A75, A86, A87, A91, A92, A98, A99, A105, A106, A114, A115, A121, A131, A136, A139, A147, A151, A153, A164, A175; 40 specimens from Bousfield 1980 stns. S4B1-4, S8B1, S13B1, S18B1, S19B1.

British Columbia — Queen Charlotte Islands: 131 specimens from Bousfield 1957 stns., E5, E9, E14a, E14b, E14c, E21, E24, E25, H4a, H5, H8a, H8b, H9, H11, W5, W15b. Northern main-

land: 35 specimens from Bousfield 1964 stns., H8, H12, H13, H17, H32, H33, H50, H56. Northern Vancouver Island: 7 specimens from Bousfield 1959 stn. 04. Smithsonian collections (USNM): Bousfield 1957 stn. H4a, 2 ♂♂, 2 ♀♀, immature. Zool. Inst. (Leningrad): Bousfield 1961 stn. A27, 1 ♂; Bousfield 1961 stn. A25, 2 ♀♀, 1 immature; Bousfield 1957 stn. E14a, 2 ♂♂, 2 ♀♀.

**Distribution:** Aleutian Islands, Alaska, (55°N, 163°W) to Quatsino Sound, Vancouver Island, B.C. (50°30'N, 128°06'W). Otradnaya Bay, Shikotan Island, Tatar Strait, Kurile Islands, USSR.

**Ecology:** A northern cold-temperate species found in the mid and low intertidal to a depth of about 15 m amongst algae and eelgrass, primarily on protected and less often exposed coasts, where summer temperatures are 10-17°C, and salinities are high, seldom brackish. Females are ovigerous June to August.

**Diagnosis:** Antenna 1 shorter than 2 (♂),

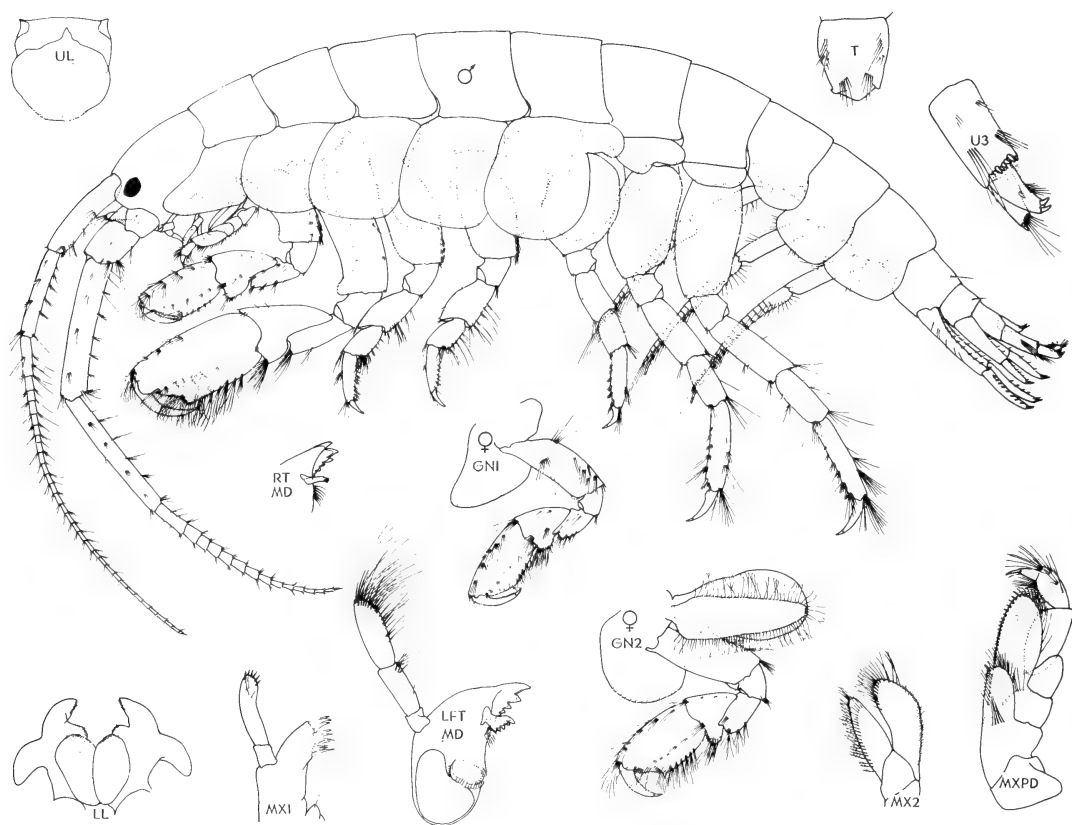


Figure 5. *Ampithoe kussakini* Gurjanova ♂ 17.5 mm; ♀ 13.0 mm, Yakoun Bay, Masset Inlet, Queen Charlotte Is., B.C. 27 August 1957

longer than 2 (♀); antenna 1 peduncle 1 with a distal ventral spine (present also in immatures); antennae 1 and 2 moderately setose. Mandibular palp segment 3 evenly rounded, setae apical and lateral; segment 2 with about 8 setae. Maxilla 1 inner plate with 1 seta, palp slender. Maxilliped outer plate teeth smooth, palp segment 2 lacking setae. Gnathopod 2 (♂), segments 4-6 elongate, palm oblique, sinuous, thumb at hind corner small or absent, groups of dense setae developing on inner side of hand at about 9 mm body length. Anterior margin of peraeopods segment 2 not strongly setose. Epimera 1-3 with a lateral ridge. Pleopods moderately setose. Uropod 3 moderately long, inner ramus with 1 medial and 4 apical spines. Colour pattern: body orange to green or brown; antennae brown and white banded. Body length at maturity: Male 9-18 mm, female 9-20 mm.

*Remarks:* There are some discrepancies between this and Gurjanova's description (types not re-examined). Her specimens are much larger

than those examined here, the male being 31 mm, the female 29 mm, yet the flagella of antennae 1 and 2 are much shorter, comprised of 15 and 6 segments respectively, as opposed to 30 and 13-14 in our specimens half their size. Gurjanova stated that the palm of the female gnathopod 2 lacks an obturator spine, an unusual feature, yet one is present in the North American specimens. The number of setae on the telson of Gurjanova's specimens is only about half the North American number. Perhaps, however, these characters reduce with age. Otherwise the eastern and western Pacific specimens show close resemblance.

*Ampithoe volki* Gurjanova 1938 ?

Figure 6.

*Ampithoe volki* Gurjanova 1938, p. 359, fig. 52; 1951, p. 899-901, fig. 624.

*Material examined:* Alaska — St. Makarius Bay, Amchitka Island (51°N, 179°W), collection of C.E. O'Clair, 1968. 1 male, 1 female, 2 immatures.

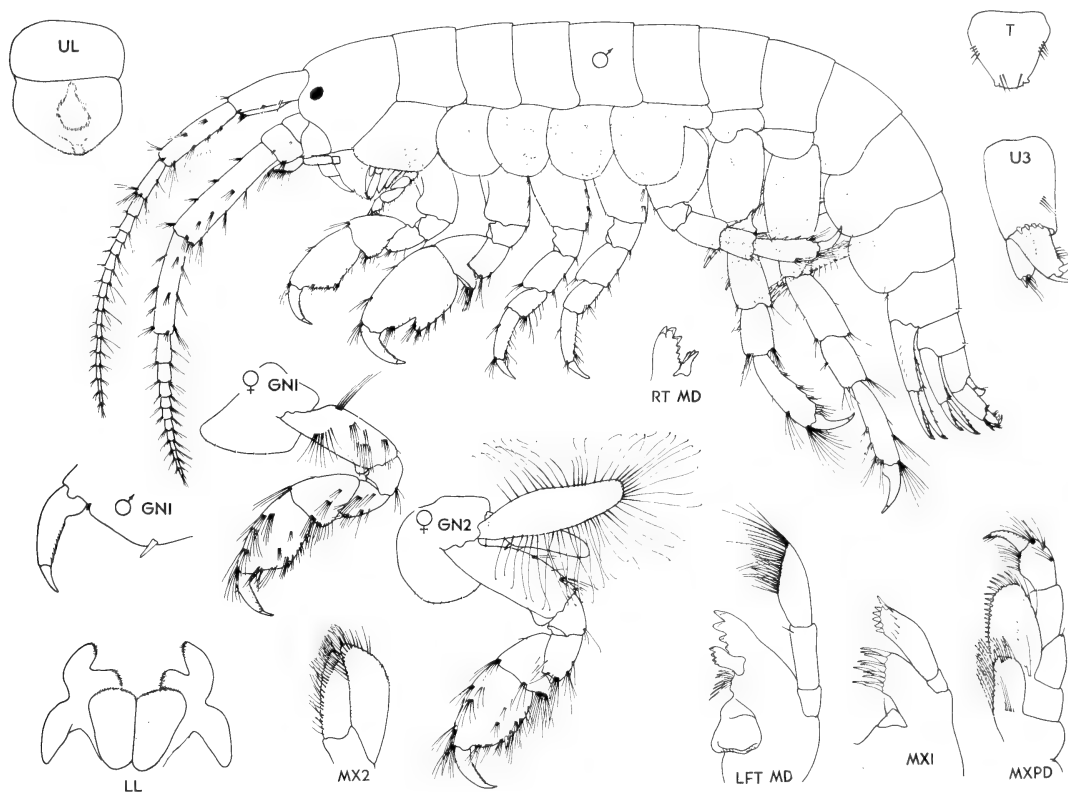


Figure 6. *Ampithoe volki* Gurjanova? ♂ 8.0 mm; ♀ 8.0 mm, St. Makarius Bay, Amchitka, Is., Aleutian Is., Alaska. 20 July 1968

**Distribution:** Amchitka Island, Alaska; Sea of Japan, Prebrazheu'e Bay region, USSR (45°N, 130°E), Tatar Strait and northern Kurile Islands.

**Ecology:** A cold temperate species inhabiting exposed coasts in tidepools overgrown with algae and in beds of *Laurencia*, intertidal and subtidal to 3 m depth.

**Diagnosis:** Antenna 1 shorter than 2 (♂), or subequal (♀); antenna 1 peduncle 1 with a postero-distal spine (absent in immatures); antennae 1 and 2 moderately setose. Mandibular palp segment 3 acutely oblique, tip pointed, setae apical; segment 2 with 1-2 setae. Maxilla 1 inner plate with 1 seta, palp moderately widened. Maxilliped outer plate teeth smooth, palp segment 2 setose. Gnathopod 2, male, segments 4-6 not greatly elongate, hand laterally incised to form a short truncate thumb which is not long enough to reach to the end of the hand.

Anterior margin of pereopods segment 2 not strongly setose. Epimera 1-3 with a slight lateral ridge. Pleopods moderately setose. Uropod 3 not greatly elongate, inner ramus with 3 apical and no medial spines. Body colour in life translucent yellowish-grayish-brownish (Gurjanova 1951). Body length at maturity: Male 8 mm, female 8 mm.

**Remarks:** Table 1 illustrates that there are several differences between these specimens and Gurjanova's types which may warrant designation of a new species name.

***Ampithoe sectimanus* n. sp.**

Figure 7.

*Ampithoe pollex*: J.L. Barnard 1954, p. 29-31, pls. 27-28 (not Kunkel 1910)

? *Ampithoe simulans*: J.L. Barnard 1965, p. 27-30, fig. 18 (not Alderman, 1936)

**Material examined:** Point east of Point Marsh,

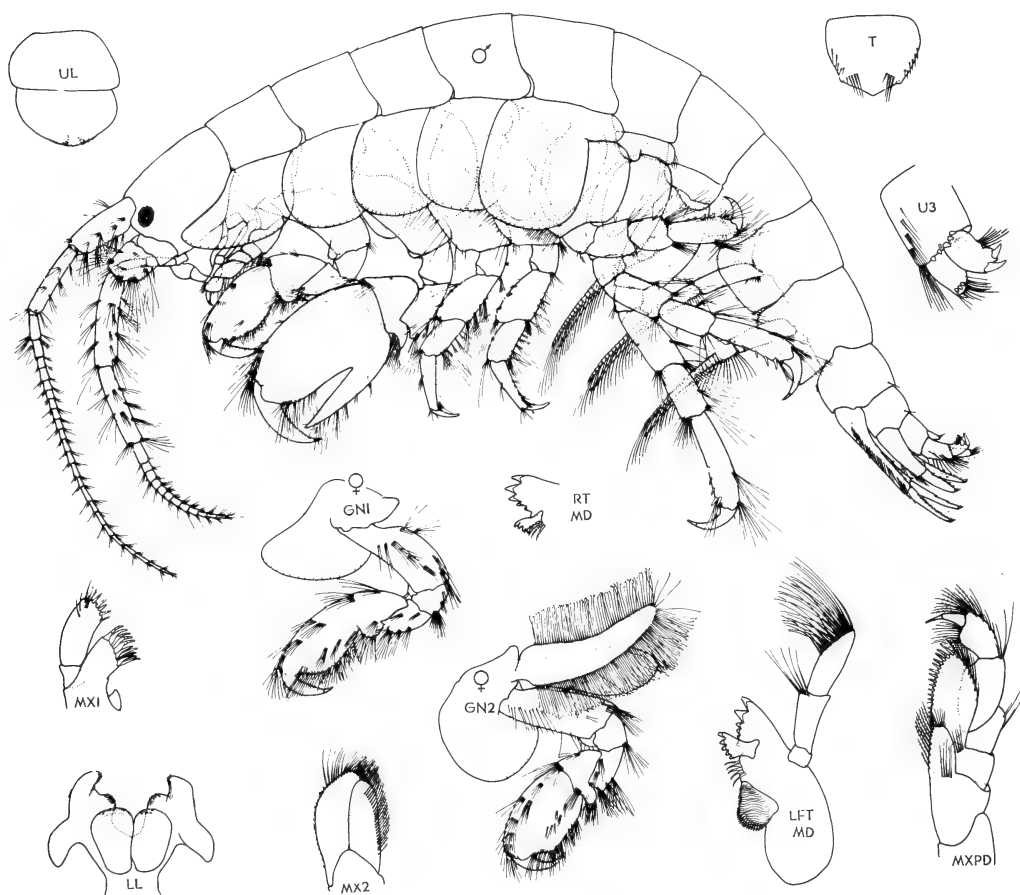


Figure 7. *Ampithoe sectimanus* n.sp. ♂ 11.0 mm; ♀ 11.5 mm, Point Marsh, Prince of Wales Is., Alaska. 1 June 1961



Prince of Wales Island, Alaska (54°43'N, 132°17'W). Bousfield stn. A6, 1 June 1961. Tide-pools and under stones. LW to MW. 9.5°C, 30.0‰. Holotype ♂ (NMC-C-1981-961); allotype ♀ (NMC-C-1981-962); paratypes (NMC-C-1981-963).

*Additional material:* Alaska — Southeastern coast: About 40 specimens from Bousfield & McAllister 1961 stns. A6 (holotype, allotype, paratypes), A98, A171-2; 5 specimens from Bousfield 1980 stns. S4B5 and S11B1.

British Columbia — Queen Charlotte Islands: About 55 specimens from Bousfield 1957 stns., W4a, W8, W12. Northern mainland: 66 specimens from Bousfield 1964 stns. H12, H50, H53. Vancouver Island and southern mainland: 9 specimens from Bousfield 1977 stns., B6a, B11b, B19a, B19b; about 30 specimens from Bousfield 1976 stns., B7, B28; 3 specimens from Bousfield 1975 stns., P5c, P17d; 174 specimens from Bousfield 1970 stns., P702, P710, P711, P712, P719; 18 specimens from Bousfield 1959 stns., 01, 03, 05, 07b, V4B, V5, N6 and cat. #2606; 6 specimens from Bousfield 1955 stn., P7; also 3 specimens from the collections of C. Haylock 1975, R.K. Lee 1971 and G.C. Carl 1934. Oregon — 1 specimen from Bousfield 1966 stn., W60, Otter Rock at Marine Gardens, Lincoln Co. Smithsonian collections (USNM): Bousfield 1961 stn. A171-2, 1 ♂, 1 ♀; Bousfield 1970 stn. P712, 3 ♂♂, 3 ♀♀, Zool. Inst. (Leningrad); Bousfield 1970 stn. P702, 1 ♂, 2 ♀♀; Bousfield 1957 stn. W12, 2 ♂♂ juveniles, 2 ♀♀.

*Distribution:* Prince William Sound, Alaska, (60°2'N, 146°47'W), south to Cape Arago, Oregon (43°30'N, 124°26'W).

*Ecology:* A cold-temperate species restricted to high salinity, exposed coasts, amongst algae on rocky headlands at low water level, in low summer temperatures (9.5°-15°C) and high salinities (23.3-33.7‰). Females ovigerous May to August.

*Description of male holotype*, 11.0 mm: Antennae 1 and 2 subequal, peduncles strongly setose; antenna 1 peduncle 1 lacking a ventral spine. Mandibular palp segment 3 acutely oblique, tip pointed, setae apical; segment 2 with 3 setae. Maxilla 1 inner plate bare, palp broad. Maxilliped outer plate teeth serrated, palp segment 2 setose. Gnathopod 2, segments 4 and 5 not greatly elongate, segment 6 enlarged, palm distally incised (beginning at 7 mm body length), to form a pointed thumb which splits

increasingly with age to more than half the length of the hand. Anterior margin of peraeopods 3-7 segment 2 strongly setose (degree and extent varies with age). Epimeron 3 with a faint indication of a lateral ridge. Pleopods strongly setose. Uropod 3 short, inner ramus with 4 apical and no medial spines. Body colour in life: mottled orange to chestnut, legs and antennae orange and white banded. Body length: male 7-10 mm, female 8.5-12.5 mm.

*Description of female allotype*, 11.5 mm: Body and appendages as in the male, except gnathopod 2 which is similar in form and somewhat larger than gnathopod 1.

*Etymology:* (L.: secti = split; manus = hand), referring to the strongly cleft palm of the male second gnathopod.

*Remarks:* *Ampithoe sectimanus* was figured by Barnard (1954) as *Ampithoe pollex* Kunkel 1910. The latter species differs in many features — smaller body size, weaker setation of antennae and peraeopods (yet stronger setation of peraeopods 3 and 4), different shape of gnathopods and near occlusion of the inner lobes of the lower lip. Barnard (1965) also figured gnathopod 2 of two male specimens from station 40a, Coal Oil Point, Goleta, California, that he called aberrant forms of *Ampithoe simulans*. The illustration of a longer palmar tooth on the hand combined with the statement that the lobes of the lower lip are well separated, indicates that these are more likely specimens of *Ampithoe sectimanus*. If so, these specimens mark the southernmost distributional limit of this species.

#### **Group of *Ampithoe rubricatoides*, *A. dalli*, *A. simulans***

Head, lateral lobe and antennal sinus shallow; eye small. Antenna 1 shorter than 2, peduncle poorly setose. Antenna 2 much heavier than antenna 1, flagellum equal in length to peduncular segments 4 and 5 together. Mandibular palp segment 3 oblique, laterally setose. Coxa 1, anterior margin straight or slightly upcurved, coxae 1 and 2 of the male shallower than 3-5; coxa 5 in both sexes, lower corners evenly rounded. Gnathopod 1, lower lobe of segment 5 narrow, less than half the length of the full segment and not produced forward under segment 6. Gnathopod 2 (♂), segment 3 not produced into an anterior lobe, palm strongly concave, with or without a small "thumb" on the hind corner. Peraeopods 3 and 4 normal, segment

4 more than half as wide as segment 2. Peraeopods 5-7 strong, slightly expanded distally, spines strong. Epimera 1-3 without a lateral ridge. Pleopods with 6-11 coupling hooks. Uropods 1 and 2, rami tipped by a single strong spine. Uropod 3 short, uncini of outer ramus strong. *Ampithoe corallina* Stout 1913, which might also be found in the northeastern Pacific, seems referable to this group.

***Ampithoe rubricatoides* Shoemaker 1938**

Figure 8. (reconstructed from Shoemaker, 1938)

*Ampithoe rubricatoides* Shoemaker 1938, p. 22, figs. 3, 4

*Ampithoe rubricatoides* Gurjanova 1951, p. 878-880, fig. 613

**Material examined:** No material available. Information extracted from Shoemaker (1938).

**Distribution:** Alaska — Aleutian Islands: Pribilof Islands (57°N, 172°W).

**Ecology:** A cold water species found subtidally at 10-18 m depth in sand and mud sediments.

**Diagnosis:** Head, antennal sinus absent, eye small. Antenna 2 moderately setose. Mandibular palp segment 2 short, less than twice the length of segment 1; one corner and a group of 4 lateral

setae; segment 3 oblique, apically setose for about  $\frac{3}{4}$  its length. Gnathopod 1 palm very oblique, passing by a scarcely perceptible angle into the hind margin; male segment 2 lacking plumose setae. Gnathopod 2 (♂), segment 5 lacking a dorsal tubercle; hand not greatly enlarged, less than twice the size of the hand of gnathopod 1; palm concave, lacking teeth, other than the normal obturator spine. Peraeopod 7 segment 6 with 5 marginal spine groups. Epimeron 3 hind margin evenly rounded. Uropods very spinose, uropod 1 peduncle with about 15 outer spines, outer ramus with about 25 spines. Uropod 3 peduncle with about 15 crown spines and 2 dorsal spines. Body length: Male 24 mm, female length not stated.

***Ampithoe dalli* Shoemaker 1938**

Figure 9.

*Ampithoe dalli* Shoemaker 1938, p. 19-22, fig. 2; Gurjanova, 1951, p. 887-890, fig. 618

*Ampithoe simulans* Barnard, 1965, p. 27-30, fig. 17 (not Alderman 1936)

**Material examined:** Alaska — Aleutian Islands: 9 specimens from the collections of C.E. O'Clair, 1972-74. Southeastern Alaska; 207 specimens

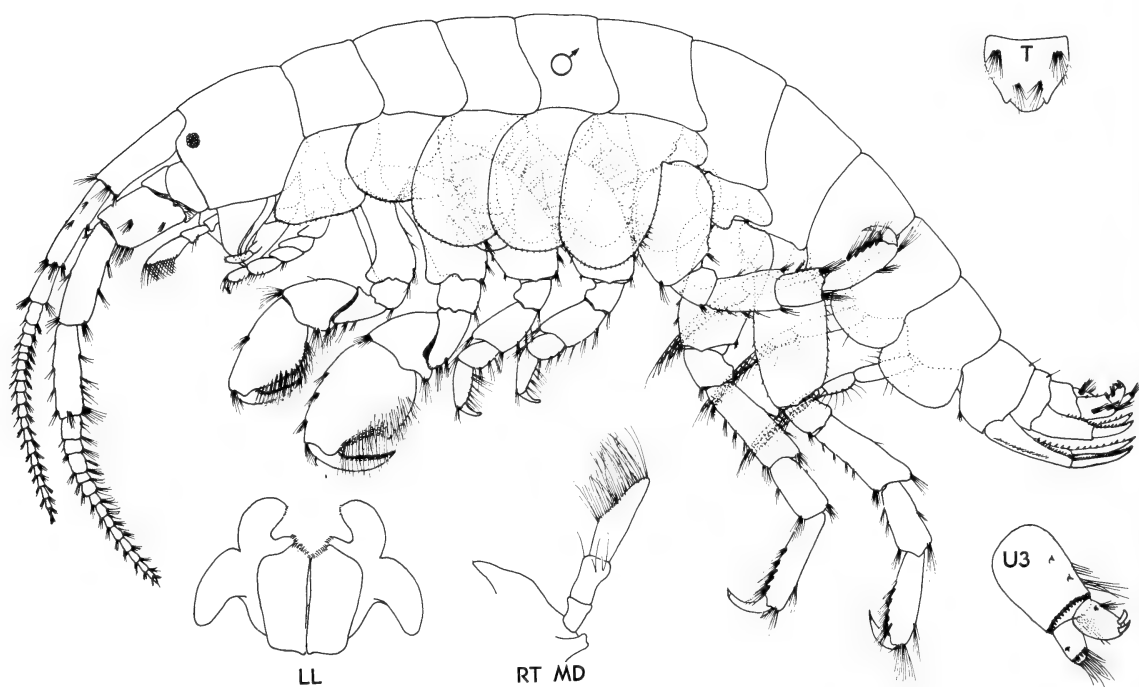


Figure 8. *Ampithoe rubricatoides* Shoemaker ♂ 24.0 mm, Kyska Is., Aleutian Is., Alaska. 1873. Reconstructed from Shoemaker, 1938

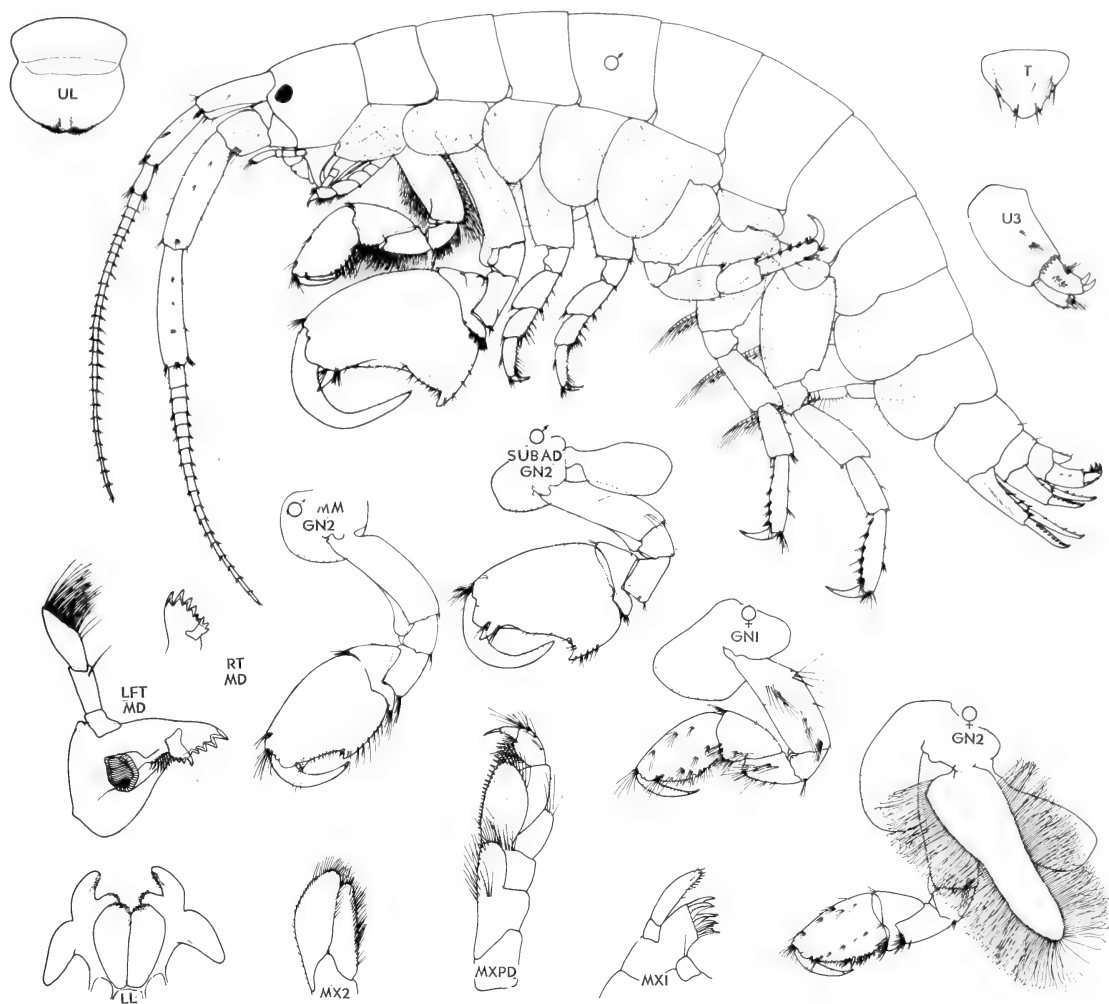


Figure 9. *Ampithoe dalli* Shoemaker ♂ 18.0 mm; ♂ subadult 11.0 mm, ♀ 20.0 mm, Kakul Narrows, Baranof Is., Alaska. 9 June 1961

from Bousfield and McAllister 1961 stns., A2, A5, A7, A18, A23, A25, A27, A33, A37, A43, A48, A68, A71, A98, A105, A115, A121; 50 specimens from Bousfield 1980 stns., S1L1, S7B4, S7B5, S8B1, S11B1, S13B1, S18B1, S20B2, S20B4, S20B5, S20B6.

British Columbia — Queen Charlotte Islands: 40 specimens from Bousfield 1957 stns., E25, H8b, H14, H15, W1, W5a, W9b, W12, W15. Northern mainland: 191 specimens from Bousfield 1964 stns., H1, H13, H29, H33, H35, H40, H44. Vancouver Island and southern mainland: 1 specimen from Bousfield 1977 stn. B12c; 33 specimens from Bousfield 1976 stns., B2, B3, B12a,

B13, B14b; 5 specimens from Bousfield 1975 stns., P5d, P18; 25 specimens from Bousfield 1970 stns., P703, P704, P705, P714, P715, P719; 2 specimens from Bousfield 1959 stns., 03, 04; 115 specimens from Bousfield 1955 stns., P2, P4, P7, F2a, F5, G1, G11, G13, M2, M5, M11; in addition, 464 specimens from the collections of J.C. Carl, S. Cross, D.V. Ellis, D. Kittle, R.K.S. Lee, C. Levings, C. Lobban, D.E. McAllister and R.I. Smith.

Washington and Oregon — 3 specimens from Bousfield 1966 stns., W5, W34, W64. Smithsonian collections (USNM): Bousfield 1961 stn. A27, 1 ♂, 1 ♂ juvenile, 1 ♀.

**Distribution:** Known authentically from Aleutian Islands, Alaska (51°N, 179°W) south to Cape Arago, Oregon (60°30'N, 124°26'W). Pacific coast of the USSR.

**Ecology:** A cold-temperate species occurring amongst algae and eelgrass on exposed and protected beaches, in tidepools, under stones and amongst log fouling organisms. Occurs in the low intertidal to 10 m depth in a wide range of salinities (10-33‰), and in summer temperatures (8-18°C). Females ovigerous March-August.

**Diagnosis:** Head, antennal sinus slight, eye small. Antenna 2 poorly setose. Mandibular palp segment 2 more than twice the length of segment 1 and bearing a single corner seta; segment 3 acutely oblique, a definite angle between apical and lateral margins, apically setose for about 1/2 its length. Gnathopod 1 palm less oblique than in *A. rubricata*, definite angle from the palm to hind margin; male segment 2 with dense, long plumose setae on the front, inner and hind margins at about 6-7 mm body length, the plumosity extending by 8-12 mm body size to the lower margins of segments 3, 4 and 5. Gnathopod 2 (♂), segment 5 with a low dorsal tubercle; hand enlarging with age, sides diverging and palm lengthening, a medial tooth forming at the dactyl hinge and another at the hind corner of the palm; dactyl increasingly curved with age, failing to meet the hind palmar tooth in old specimens. Peraeopod 7 segment 6 with 5-7 marginal spine groups (depending on age). Epimeron 3 rounded, hind corner with slight indentation holding a small seta. Uropod 1 with not more than 6 spines on the outer peduncle and 10 spines on the outer ramus. Uropod 3 with 6 crown spines and no central spines. Body colour in life: uniformly green to brown speckled. Body length at maturity: male 8-18 mm, female 7-20 mm.

A plot of the body length of 272 specimens against geographic distribution showed a general increase in body size with latitude. In latitude 45°-52°, mean length was 10.8 mm (♂) (range 8-17 mm), 10.5 mm (♀) (range 7-15 mm). In latitudes 53°-65°, mean length was 12.2 mm (♂) (range 7-19 mm), 14.1 mm (♀) (range 7-20 mm). In the female, the presence of brooding immatures was found to occur at a size at least 1.5 mm greater than

in the condition where the brood pouch was empty but brood lamellae were setose, indicating that a moult occurred between these two stages. Some seasonal differences in size of maturity were also observed, individuals in the spring (presumably having overwintered) being about 1-2 mm larger than later individuals which presumably were early offspring able to mature more quickly in warmer summer water. This indicates that gonadal growth requires a higher temperature than does somatic growth.

**Remarks:** Barnard (1954) synonymized *Ampithoe dalli* with *Ampithoe simulans*, in the belief that *A. dalli* represented the mature form of *A. simulans*, the transformation occurring at about 15 mm. However, his conclusions were based on the evidence of subadult male specimens which do resemble each other closely but diverge with age. The characters which distinguish these species are body size at maturity, eye size, shape of the mandibular palp, degree of plumosity of male gnathopod 1, shape of male gnathopod 2, spination of peraeopod 7, shape of epimeron 3 and body colour.

#### *Ampithoe simulans* Alderman 1936

Figure 10.

*Ampithoe simulans* Alderman 1936, p. 68-79, figs. 44-47; J.L. Barnard, 1954, p. 33-34, 1 fig.; not J.L. Barnard, 1965, p. 27-30, fig. 17; ? J.L. Barnard, 1969b, p. 85

**Material examined:** Alaska — Aleutian Islands: 1 specimen from the collection of C.E. O'Clair, 1972 (St. Makarius Bay, Amchitka Island). Southeastern Alaska: 23 specimens from Bousfield and McAllister 1961 stns., A99, A114, A147, A168; 2 specimens from Bousfield 1980 stn. S18B1.

British Columbia — Queen Charlotte Islands: 3 specimens from Bousfield 1957 stns., W1, W9a. 1 specimen from collection of M. Frazer, 1935. Northern mainland: 9 specimens from Bousfield 1964 stns., H12, H16. Vancouver Island: 2 specimens from Bousfield 1975 stns., P5a; 25 specimens from Bousfield 1970 stns., P702, P710, P712, P715; 2 specimens from Bousfield 1959 stn., N1; 4 specimens from the collections of R.K. Lee, 1973 and N.A. Powell, 1966. Washington and Oregon — 10 specimens from Bousfield 1966 stns.,

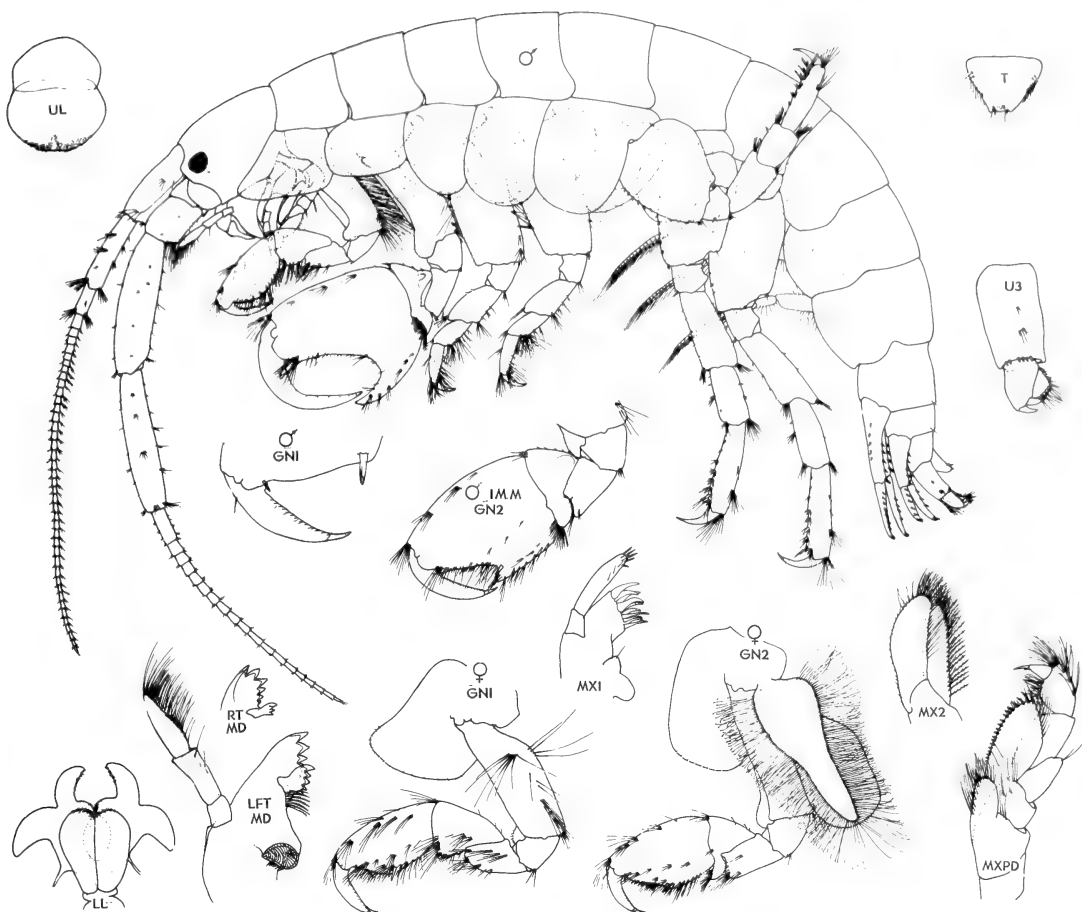


Figure 10. *Ampithoe simulans* Alderman ♂ 18.0 mm; ♂ subadult 13.0 mm; ♀ 15.5 mm, Gonzales Bay, Victoria, B.C. 29 July 1970

W34, W35, W50; 1 specimen from the collection of N. McDaniel.

Smithsonian collections (USNM): R.K. Lee stn. 150E, 1 ♂, 1 ♀.

**Distribution:** Known authentically from St. Makarius Bay, Amchitka Island, Alaska (51°N, 179°W) south to Cannon Beach, Clatsop Co., Oregon (45°54.5'N, 123°58'W).

**Ecology:** A cold temperate species occurring from low water level to 4 m depth, amongst algae and eelgrass on semi-protected and exposed coasts in summer temperatures 10-16°C, salinities 29-34‰, occasionally in brackish water.

**Diagnosis:** Head, antennal sinus slight, eye larger than in *A. dalli*. Antenna 2 poorly setose.

Mandibular palp segment 2 more than twice the length of segment 1 and bearing 1 or 2 setae; segment 3 very oblique, passing by a barely perceptible angle into the lower margin and setose for nearly the full length. Gnathopod 1 palm less oblique than in *A. rubricata*, palm verging into the hind margin at a definite angle; male segment 2 with a few plumose setae on the hind margin only (beginning at 11-15 mm body length), but plumosity not extending to other segments. Gnathopod 2 (♂), segment 5 with a low dorsal tubercle; hand enlarging with age and sides diverging, palm becoming increasingly concave, hind corner lengthening to form a broad tooth, a smaller medial tooth developing at the dactyl hinge; dactyl increasingly curved

with age but always meeting the long hind tooth. Peraeopod 7 segment 6 with 6-8 marginal spine groups (depending on age). Epimeron 3 rectangular, hind corner indented more strongly than in *A. dalli*. Uropod 1 with not more than 6 spines on the outer peduncle and 10 spines on the outer ramus. Uropod 3 with 6 crown spines and no central spines. Body colour in life: uniformly green to brown speckled. Body length at maturity: Male 11-23 mm, female 12-30 mm.

*Remarks:* Alderman's description of the type male is based on the characteristics of a subadult: viz. the absence of plumose setae on gnathopod 1, a hardly enlarged gnathopod 2 that lacks a hinge tooth but retains a serrated dactyl. His specimens were 12-24 mm in length, a size at which plumosity and enlargement of the gnathopod would have occurred if the specimen had been *A. dalli*.

The two palmar teeth of the male gnathopod 2 of *A. dalli* and *A. simulans* grow at the location of and eventually replace the obturator spine and slender dactyl hinge spine (see Fig. 10). The large teeth probably prevent the enlarged dactyl from crimping the female during amplexus.

Barnard (1965) suggested that *Ampithoe simulans* is probably synonymous with *Ampithoe corallina* Stout (1913), in the belief that Stout might have confused the male with a female because of the undifferentiated second gnathopod of the male. However, Stout mentioned that females of 6-8 mm were carrying eggs, indicating that this species matures at a much smaller size than *A. simulans*. *A. corallina* differs also in the following: head very deep and broad, relatively strongly setose antennae, large number of segments in antennal flagella, lower lip outer lobes subequal in size, mandibular palp obliquely acute with only 6 setae.

The two aberrant specimens of *A. simulans* shown by Barnard to have a deeply incised hand

of gnathopod 2 are indeed not this species but males of *Ampithoe sectimanus* n.sp.

### Genus *Peramphithoe* new genus

Type species: *Ampithoe femorata* Krøyer 1845

Component species: *A. orientalis* Dana 1853, *A. humeralis* Stimpson 1864, *A. eoa* Brüggén 1907, *A. falsa* K.H. Barnard 1932, *A. annenkovae* Gurjanova 1938, *A. lindbergi* Gurjanova 1938, *A. mea* Gurjanova 1938, *A. plea* Barnard 1965, *A. tea* Barnard 1965, *A. spuria* Krapp-Schickel 1978, *A. aorangi* Barnard 1979, *P. humeralis* (not Stimpson 1864) of Griffiths, 1979, *P. lessoniophila* n.sp.

*Diagnosis:* Head lobe produced, antennal sinus present. Antenna 1 accessory flagellum absent. Mandibular palp moderately weak. Maxilla 1 palp slender. Gnathopod 1, palm transverse, coxa 1 not produced forward. Gnathopod 2 subchelate, equal to or larger than 1. Peraeopods 3 and 4, segment 2 strongly inflated. Peraeopods 5-7, segment 6 not distally expanded, spines usually not restricted to the antero-distal region. Uropod 1 peduncular process well developed. Uropod 3, outer ramus with two hooked uncini. Telson with two small apical cusps.

About 14 species, arctic-boreal to tropical, littoral.

*Etymology:* From the Greek, *pera* meaning beyond or across, referring both to the transverse form of the first gnathopod and the advanced form in relation to *Ampithoe*. The correct spelling of '*Ampithoe*' is herein applied as derived from the Greek *amphi* = around, both, and *thoë* = quick.

Northeastern Pacific species: *Peramphithoe humeralis* (Stimpson 1864), *P. mea* (Gurjanova 1938), *P. lindbergi* (Gurjanova 1938), *P. tea* (Barnard 1965), *P. plea* (Barnard 1965).

### Key to Species of *Peramphithoe* of the Northeastern Pacific

1. Body large, 19-35 mm at maturity. Antenna 2 flagellum slender, proximal segments not fused. Gnathopod 1, segment 5 shorter than segment 6. Peraeopod 5, segment 4 longer than 5. Male gnathopod 2 hardly enlarged, dactyl less than twice the length of the dactyl of gnathopod 1 ..... 2
- Body small, 6-12 mm at maturity. Antenna 2 flagellum heavy, proximal segments fused. Gnathopod 1, segment 5 equal to or longer than segment 6. Peraeopod 5, segments 4 and 5 subequal. Male gnathopod 2 enlarged, dactyl more than twice the length of the dactyl of gnathopod 1 ..... 3

2. Gnathopod 1, segment 5 longer than 6. Gnathopod 2 (both sexes) subequal to 1, palm transverse; segment 5 longer than deep and as long as segment 6. Peraeopod 7 larger and about one third longer than peraeopod 6 ..... *Peramphithoe humeralis* (Stimpson 1864) (p. 61)  
Gnathopod 1, segment 5 about equal in length to 6. Gnathopod 2 (both sexes) larger than 1, palm oblique; segment 5 not longer than deep and shorter than segment 6; peraeopod 7 hardly larger than peraeopod 6 ..... *Peramphithoe mea* (Gurjanova 1938) (p. 63)
3. Antenna 1 peduncle 1 lacking a postero-distal spine. Antenna 2 slender and nearly as long as antenna 1. Gnathopod 1 dactyl overlapping the palm by hardly more than the length of the nail. Gnathopod 2 (♂), hand rectangular, dactyl sinuous, palm with a low rounded palmar process at dactyl hinge ..... *Peramphithoe plea* (Barnard 1965) (p. 67)  
Antenna 1 peduncle with a posterodistal spine in mature individuals. Antenna 2 heavy, less than  $\frac{3}{4}$  length of antenna 1. Gnathopod 1 dactyl overlapping the palm by considerably more than the length of the nail. Gnathopod 2 (♂) proximally broader, dactyl evenly curved, palm with or without process at hinge ..... 4
4. Antenna 2 about  $\frac{3}{4}$  the length of antenna 1; flagellum  $1\frac{1}{2}$  times the length of peduncle 5, proximal segments of flagellum fused in pairs. Gnathopod 2 (♂), palm with tubercle at dactyl hinge, dactyl reaching with age to the length of the hand .....  
..... *Peramphithoe tea* (Barnard 1965) (p. 65)  
Antenna 2 about  $\frac{1}{2}$  length of antenna 1; flagellum about equal to the length of peduncle 5, proximal 5-6 segments of flagellum fused together. Gnathopod 2 (♂), palm lacking tubercle at hinge, dactyl never more than half the length of the hand .....  
..... *Peramphithoe lindbergi* (Gurjanova 1938) (p. 64)

The Eastern North Pacific species of *Peramphithoe* are divisible into two groups, which may later warrant formal taxonomic recognition —

1) *P. humeralis*, *P. mea*

2) *P. lindbergi*, *P. tea*, *P. plea*

Characteristics which order the species are, progressive decrease in body size, compression of the antenna 2 flagellum and increase in sexual dimorphism. This may represent an evolutionary gradient.

#### Group of *Peramphithoe humeralis* and *P. mea*

Body large, 19-35 mm at maturity. Eye medium to small. Antenna 2 flagellum slender, proximal segments not fused. Lower lip outer lobes, apical longer than medial. Gnathopod 1, segment 5 longer than or equal to 6. Gnathopod 2 not greatly enlarged, scarcely sexually dimorphic. Peraeopods 3 and 4, segment 4 barely extending over segment 5. Peraeopod 5, segment 4 longer than 5. Peraeopods 6 and 7 anterior and posterior setae short, about equal in length. Pleopods with 8-9 coupling hooks.

#### *Peramphithoe humeralis* (Stimpson 1864)

Figure 11.

*Amphithoe humeralis* Stimpson 1864, p. 156;

Calman, 1898, p. 271-273, pl. 33, fig. 4;

Holmes, 1904, p. 241; Hewatt, 1946, p. 199, 204.

*Amphithoe humeralis*: Stebbing, 1906, p. 636;

J.L. Barnard, 1954, p. 29; J.L. Barnard, 1965, p. 7, figs. 2, 3; J.L. Barnard 1969b, p. 83, not Griffiths, 1979, p. 131-138, figs. 1-3.

*Material examined*: Alaska — southeastern coast: 36 specimens from Bousfield and McAllister 1961 stns., A3, A6, A59, A75, A80, A81, A83, A131, A151, A168, A171-2, A174, A175; 1 specimen from Bousfield 1980 stn. S23F1. British Columbia — Queen Charlotte Islands: 11 specimens from Bousfield 1957 stns., E5, H2a, H3, H14, W1; 5 specimens from the collection of W. Spreadborough. Northern mainland: 6 specimens from Bousfield 1964 stns., H3, H7, H26, H30, H47, H65. Vancouver Island and southern mainland: 2 specimens from Bousfield 1977 stns., B6b, B8; 1 specimen from Bousfield 1975 stn., P5c; 18 specimens from Bousfield 1970 stns., P710, P711, P712, P715; 3 specimens from Bousfield 1959 stns., 015, V4b; 3 specimens from Bousfield 1955 stns., F8, P7; 23 specimens from the collections of J.F.L. Hart, D. Kittle, N.A. Powell, D.B. Quayle, D. Zittin. Washington — 1 specimen from Bousfield 1966 stn., W35; 4 specimens from the collection of R.M. O'Clair, 1974. Smithsonian collections (USNM): Bousfield 1961 stn. A75, 2 ♂♂, 1 ♀ subadult, 1 ♀ juvenile, 3 immatures; stn. A6, 1 ♀, 1 immature.

*Distribution*: Prince William Sound, Alaska (60°40'N, 145°36'W), south to Guadalupe Island, Baja California.

*Ecology*: Occurs amongst eelgrass and kelp,

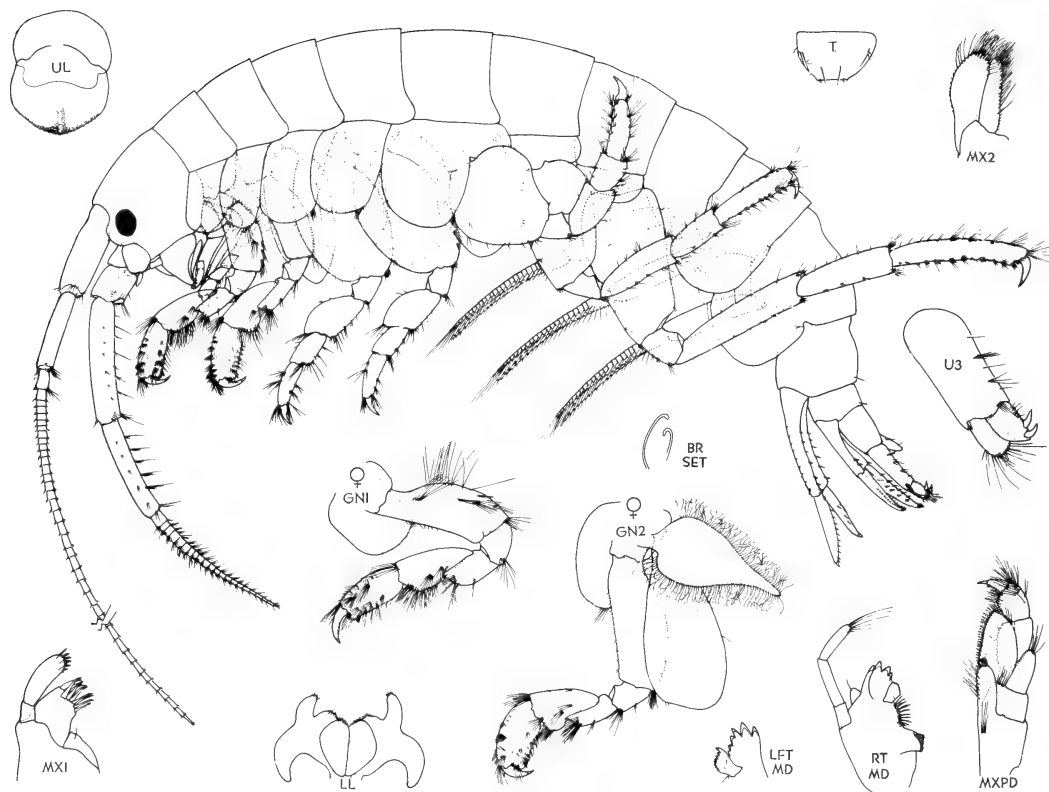


Figure 11. *Peramphithoe humeralis* (Stimpson) ♂ 15.0 mm; ♀ 19.0 mm, Trevor Channel, Barkely Sound, Vancouver Is., B.C. 25 May 1977

curling a frond around itself to form a tube. Several animals, such as a brood of young accompanying the parent may use the same tube (Jones, 1971). Mainly intertidal in the north, subtidal in California to a depth of 70 m. Usually in high salinity, exposed or semi-protected shores where summer water temperature is 9.5-14.5°C, salinity 14.3-32.7‰. Females ovigerous June to August.

**Diagnosis:** Eye medium. Gnathopod 1, segment 5 longer than segment 6. Gnathopod 2, both sexes, not enlarged, palm transverse, segment 5 equal to or longer than 6, hind lobe broad and rounded. Peraeopod 5 segment 2 nearly as broad as long, lower hind edge concave. Peraeopod 7 much stronger than 6 and about a third longer, segment 6 with about 12 spine groups. Uropod 3 peduncle long, more than twice the length of the rami. Body colour in life: uniformly orange to brown. Body length at maturity: male up to

34.5 mm, penial papillae developing at 5 mm; female 19-35 mm.

**Remarks:** Superficially, an immature specimen may resemble the female or immature of another species. If the specimen is 8 mm or greater it can be recognized within the genus by the lack of brood plates and unaltered gnathopod 2. Other distinguishing features are the long segment 5 of gnathopods 1 and 2, slender antenna 2 and long peraeopod 7. The South African *Ampithoe humeralis* of Griffiths (1979) differs from the North American type in the form of the antennae, coxae, gnathopods, peraeopods 5-7, uropod 3, mandibular palp, lower lip and size of maturity. These differences are sufficient to designate the South African specimens as a new species. Its habits are similar to those of the North American *P. humeralis* in rolling a kelp blade into a tube and living in a colony. The upper walls of the tube are consumed by the



occupants, necessitating progressive extension of the tube downwards (Jones, 1971).

***Peramphithoe mea* (Gurjanova 1938)**

Figure 12.

*Amphithoe mea* Gurjanova 1938, p. 361-364, fig. 53; 1951, p. 882-885, fig. 616; ? J.L.

Barnard, 1966, p. 60

**Material examined:** Alaska — Aleutian Islands: Stag Point, Deer Island, 1 male from the collection of P. McRoy and P.A. Lebednik, 1970; Cold Bay, Amchitka Island, 1 male, 2 immature females from the collection of C.E. O'Clair 1970.

**Distribution:** Aleutian Islands, Alaska (51°N, 179°W); Japan Sea (45°N, 130°E).

**Ecology:** A cold water species found amongst eelgrass and algae at 5-60 m depth, rarely intertidal.

**Diagnosis:** Eye small. Gnathopod 1, segment 5 about equal in length to segment 6. Gnathopod 2,

both sexes, larger than 1, palm oblique; segment 5 shorter than 6, narrowed into an acute hind lobe. Peraeopod 5 segment 2 slender, longer than wide, lower hind edge evenly rounded. Peraeopod 7 little stronger than 6, segment 6 with about 9 spine groups. Uropod 3 peduncle normal, twice the length of the rami. Body length at maturity: male 18-22 mm, female probably about the same.

**Remarks:** The specimens examined closely resemble Gurjanova's holotype but lack a spine on the postero-distal margin of antenna 1, peduncle 1. In view of the large size reached by this species (18-22 mm), the probability, as suggested by Barnard (1965), that *P. mea* is simply an early growth stage of the much smaller (maximum 8 mm) *P. annenkovae* is highly unlikely.

Barnard's (1965) inclusion of his *Ampithoe* sp., within *P. mea* is unjustified. This species is only 8 mm yet has a more strongly developed second gnathopod resembling that of *P. lindbergi*, a very large eye, shorter segment 5 on the first

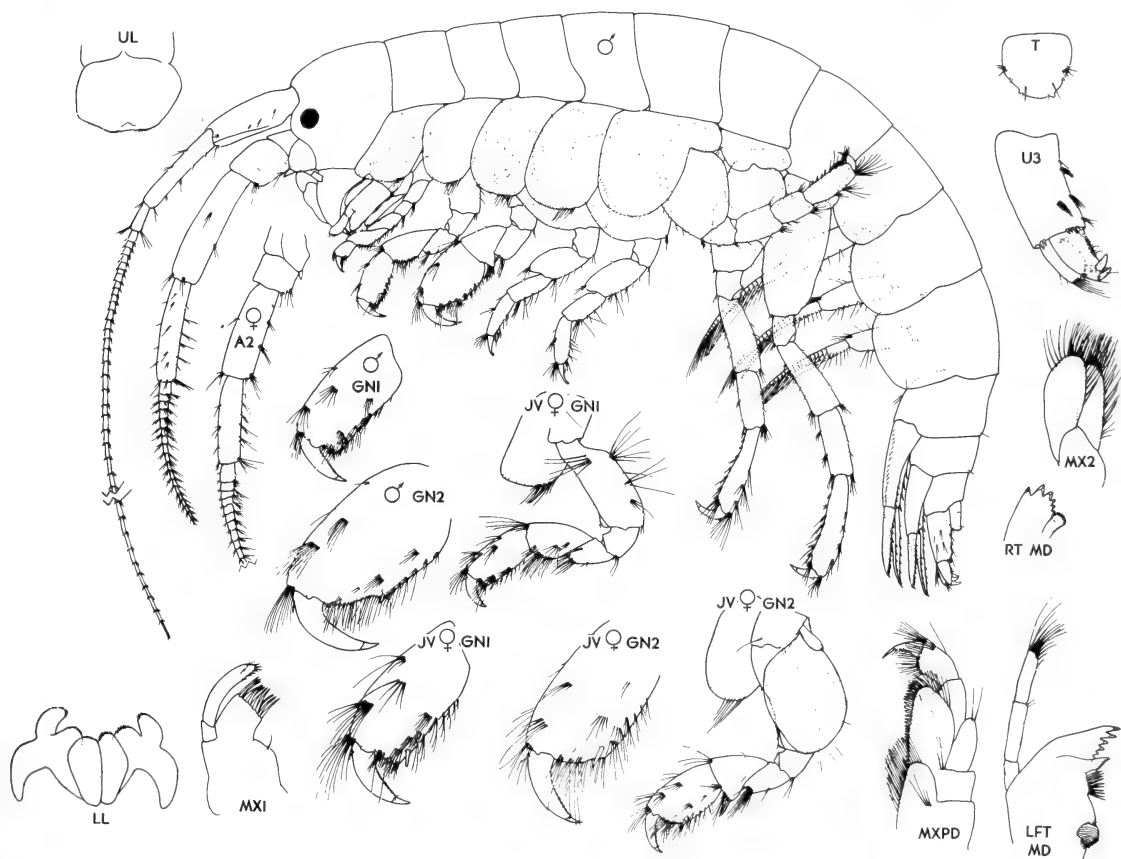


Figure 12. *Peramphithoe mea* (Gurjanova) ♂ 18.0 mm, Deer Is., Aleutian Is., Alaska. 17 Sept. 1970

gnathopod, much more expanded segment 2 and shortened segment 4 on pereopod 5 and generally more setose appendages.

Barnard's (1969b) inclusion of his Oregon *Ampithoe eoa* (Barnard 1954, not *P. eoa* (Brüggen 1970)) is similarly not justified. At 10 mm the male gnathopod is greatly enlarged, similar in shape to that of *P. tea* with two palmar tubercles, segment 5 of the first gnathopod is shorter than segment 6 and more strongly lobed, segment 4 of pereopods 3 and 4 are more strongly expanded, segment 2 of pereopod 5 is broader than deep and segment 4 is subequal to 5, uropod 2 peduncular process is very small, uropod 3 peduncle bears a central spine, the appendages are more strongly setose, and the outer lobes of the lower lip are equal in length.

*Peramphithoe eoa* (Brüggen 1907) is probably also a separate species, rather than a later growth stage as Barnard (1965) suggested. In this species the apical lobes of the lower lip are much longer than the medial, the palp of maxilla 1 is broader and more spinose, the peduncle of uropod 3 is

much longer, the gnathopod 2 of the female is less oblique and the palm crenulate, and in the male the hand of the second gnathopod is rectangular and the dactyl much longer, reaching back to segment 4.

#### Group of *Peramphithoe lindbergi*, *P. tea* and *P. plea*

Body small, 6-12 mm at maturity. Eye moderately large. Antenna 2 flagellum heavy, 5-6 proximal segments fused. Lower lip outer lobes, apical and medial subequal. Gnathopod 1, segment 5 shorter than 6. Gnathopod 2 enlarged, strongly sexually dimorphic. Pereopods 3 and 4, segment 4 extending downwards over segment 5. Pereopod 5, segments 4 and 5 subequal. Pereopods 6 and 7, posterior setae longer than anterior setae. Pleopods with 5-6 coupling hooks.

#### *Peramphithoe lindbergi* (Gurjanova 1938)

Figure 13.

*Ampithoe lindbergi* Gurjanova 1938, p. 351-354, fig. 49; 1951, p. 892-895, fig. 620

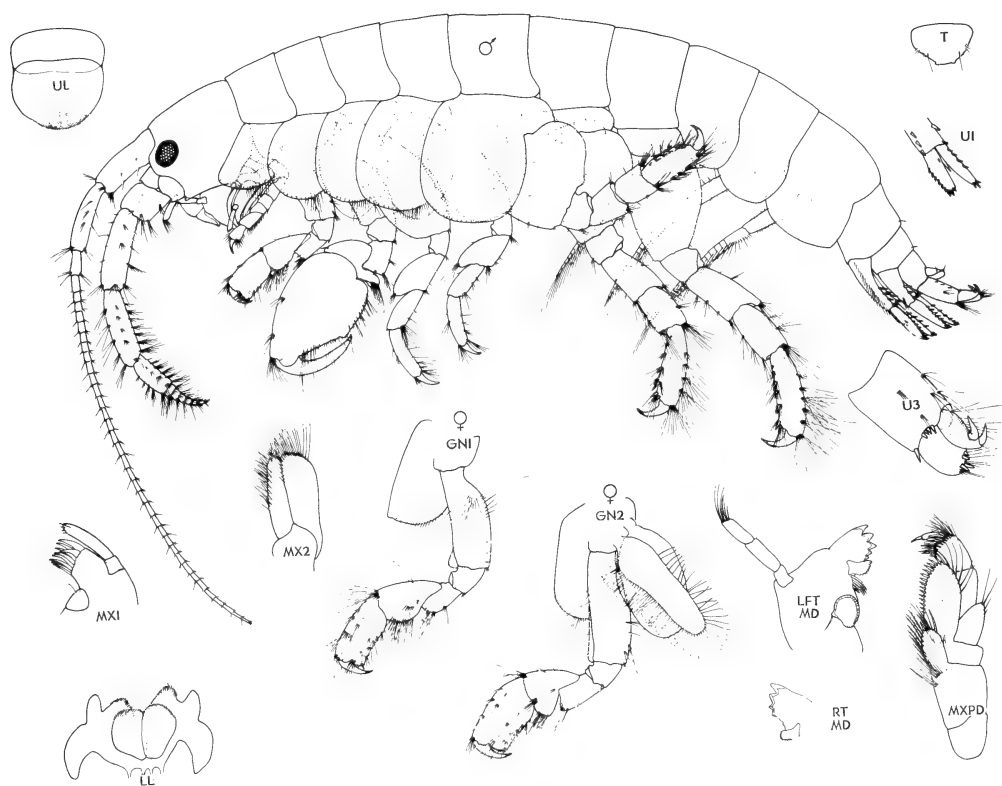


Figure 13. *Peramphithoe lindbergi* (Gurjanova) ♂ 11.0 mm; ♀ 10.0 mm, Haines Is., Barkley Sound, Vancouver Is., B.C. 8 August 1975

*Ampithoe femorata* Krøyer 1845: J.L. Barnard, 1952, p. 24-28, pls. 6, 7 (not Krøyer, 1845)

*Ampithoe lindbergi*: J.L. Barnard, 1965, p. 12-15, figs. 6, 7; 1969b, p. 83, 84

**Material examined:** Alaska — southeastern coast: 37 specimens from Bousfield and McAllister 1961 stns., A68, A70, A80, A86, A90, A92, A115, A131, A151, A174, A175.

British Columbia — Queen Charlotte Islands: 13 specimens from Bousfield 1957 stns., E25, H4a, H9, H11, W2. Northern mainland: 20 specimens from Bousfield 1964 stns., H4, H5, H17, H29, H33, H47, H53, H65. Vancouver Island and southern mainland: 4 specimens from Bousfield 1977 stn., E3; 1 specimen from Bousfield 1975 stn., P25; 2 specimens from Bousfield 1970 stns., P715, P721; 1 specimen from Bousfield 1964 stn., H43; 15 specimens from Bousfield 1959 stns., N1, 011, V5, V10, V17, V19, V20; 1 specimen from Bousfield 1957 stn. P2; 3 specimens from Bousfield 1955 stns., F2, F6; 15 specimens from the collection of L. Daniels 1975. Smithsonian collections (USNM): Daniels 1975 collection 2 ♂♂, 1 ♀, 1 ♀ subadult.

**Distribution:** Prince William Sound, Alaska (60°43'N, 146°7'W) south to Corona del Mar, California (35°5'N, 118°W); Bering Sea, Okhotsk Sea, Japan Sea (45°N, 130°E).

**Ecology:** Found amongst eelgrass and algal holdfasts at low water level to 18 m depth on exposed and protected coasts. Summer temperatures: 9.8-17.5°C, salinity 14.8-33+‰. Females ovigerous June to September.

**Diagnosis:** Body stout. Antenna 1 peduncle 1 with a postero-distal spine in mature individuals. Antenna 2 short and stout, 1/2 length of antenna 1; flagellum strongly setose, proximal 4-7 segments of flagellum fused. Gnathopod 1 dactyl overlapping the palm by considerably more than the length of the nail. Gnathopod 2 (♀), lower lobe of segment 5 pointed. Gnathopod 2 (♂), hand broadened, palm oblique, somewhat concave but without a tubercle at the dactyl hinge, dactyl evenly curved, never extending more than half the length of the hand. Peraeopod 5, lower hind edge of segment 2 straight or concave. Peraeopods 6 and 7 moderately to strongly setose, segment 2 proximally broadened. Uropods 1 and 2, rami broad. Body colour in life: uniformly yellow to olive green. Antennae yellow, red and white banded. Body length at maturity: Male 6-10.5 mm, female 6.5-12.5 mm.

**Remarks:** The length of the flagellum of

antenna 2 is quite variable and the loss of segments in the male as described by Barnard (1965) seems to represent a difference in the degree of segment fusion. A count of the number of setal bundles on flagellum 2 of 22 individuals gave a value of 8 in 7 mm specimens, to 12-14 in 10-12 mm specimens, consistently about 2 bundles less than in *Peramphithoe tea*. Immatures and females which lack antennae 2 are very difficult to distinguish from *P. tea*.

*P. lindbergi* cannot be a younger stage of *P. annenkovae* or *P. plea*, as Barnard (1965) suggested, in view of the differences stated herein, the nearly identical range in size at maturity of *P. plea* (7-10 mm), and the smaller size at maturity of *P. annenkovae* (max. 8 mm).

### *Peramphithoe tea* (Barnard 1965)

Figure 14.

*Ampithoe tea* Barnard 1965, p. 30-34, figs. 19-21; ? 1969b, p. 85

**Material examined:** Alaska — southeastern coast: 10 specimens from Bousfield and McAllister 1961 stns., A3, A8, A18, A91, A92, A96, A136, A164, A171-2; 8 specimens from Bousfield 1980 stns., S1L1, S18F3, S23F1.

British Columbia — Queen Charlotte Islands: 7 specimens from Bousfield 1957 stns., H4a, E14a, W14. Northern mainland: 46 specimens from Bousfield 1964 stns., H8, H12, H22, H25, H26, H30. Vancouver Island and southern mainland: 3 specimens from Bousfield 1977 stns., B7a, B21b; 3 specimens from Bousfield 1975 stns., P5b, P25; 2 specimens from Bousfield 1970 stns., P706, P712; 11 specimens from Bousfield 1955 stns., F1, P6a. In addition, 9 specimens from the collections of D.V. Ellis, J.F.L. Hart, R.K. Lee, N.A. Powell, J.W. Scoggan and C.H. Young and W. Spreadborough.

Smithsonian collections (USNM): Bousfield 1961 stn. A91, 1 ♂; Bousfield 1961 stn. A92, 1 ♀.

**Distribution:** Prince William Sound, Alaska (60°46'N, 146°31'W), south to Baja California (27°N, 115°W).

**Ecology:** Intertidal to a depth of 67 m, amongst algae on exposed and semi-protected high salinity coasts, in summer temperatures of 9.7-14.5°C and salinities 17.0-33+‰. Females ovigerous May to August.

**Diagnosis:** Body relatively stout. Antenna 1, peduncle segment 1 with a postero-distal spine in mature individuals. Antenna 2 heavy, about 3/4 the length of antenna 1, flagellum moderately

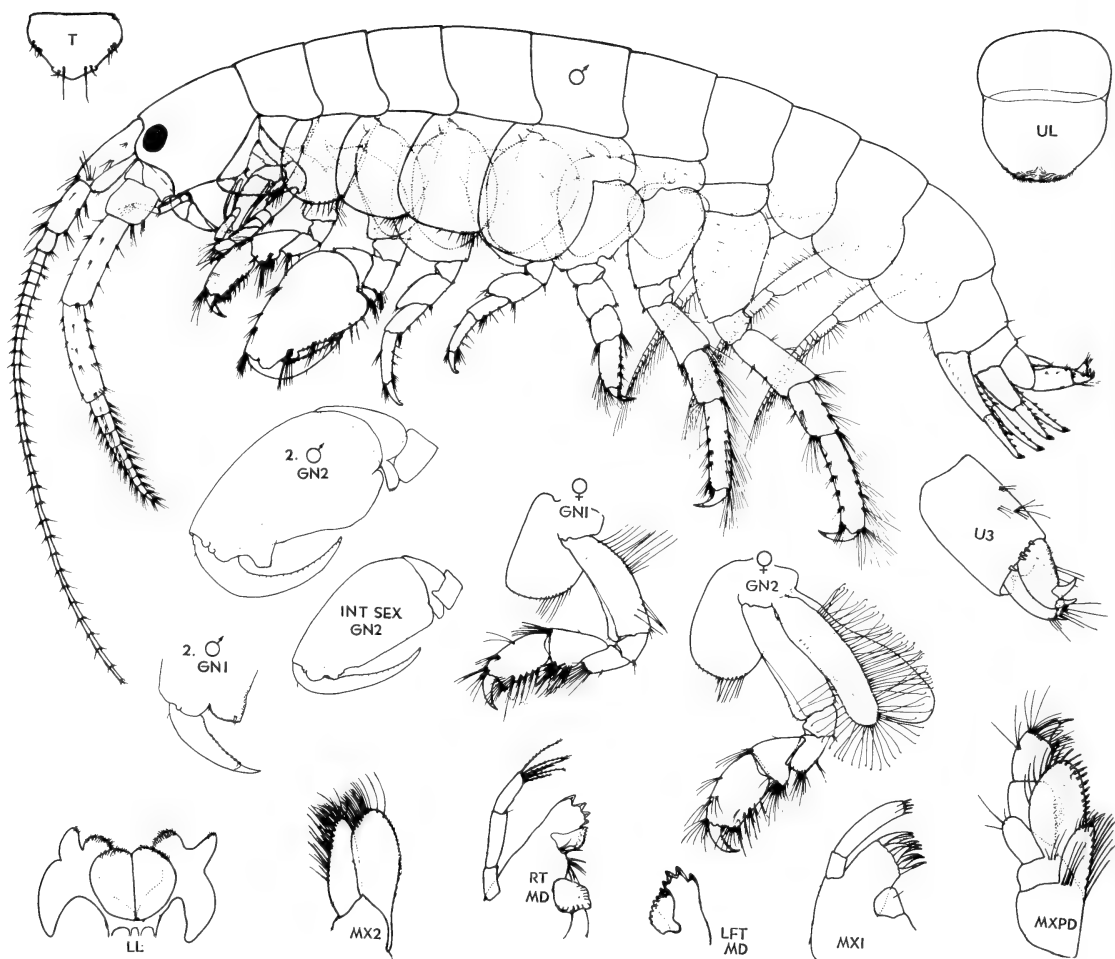


Figure 14. *Peramphithoe tea* (Barnard) ♂ 8.0 mm; ♀ 7.5 mm, Whiffen Spit, Sooke, Vancouver Is., B.C. 11 August 1969. Intersex, Yakoun Bay, Queen Charlotte Islands, B.C.

setose, proximal segments of flagellum fused in pairs. Gnathopod 1 dactyl overlapping the palm by considerably more than the length of the nail. Gnathopod 2 (♀), lower lobe of segment 5 pointed. Gnathopod 2 (♂), hand broadened, palm crenulate; at about 7.5 mm body length, palm developing a square or crenulate tubercle near the dactyl hinge. Dactyl evenly curved or slightly sinuous, increasing with age to the full length of the hand. Peraeopod 5, lower hind edge of segment 2 straight or concave. Peraeopods 6 and 7 moderately setose, segment 2 proximally broadened. Uropods 1 and 2, rami broad. Body length at maturity: male 7.5-12 mm, female

6-10 mm.

*Remarks:* The male illustrated herein, the same size as Barnard's holotype, has a much shorter dactyl on the second gnathopod and is less strongly setose. In no specimens in this collection is the dactyl more than  $\frac{3}{4}$  the length of the palm, although body lengths are comparable.

The tubercle in the palm of the male second gnathopod of this species and *P. plea* probably arises from the obturator spine and may act to prevent the dactyl from closing too tightly. The first gnathopod sometimes appears to be parachelate, a tendency that Barnard (1970) noted in a new Hawaiian species.

*Peramphithoe plea* (Barnard 1965)

Figure 15.

*Ampithoe plea* Barnard 1965, p. 15-20, figs. 9, 10

**Material examined:** British Columbia — Queen Charlotte Islands: 2 immatures from Image Point, Skidegate Inlet (Bousfield, 1957 collection, stn. E5). Vancouver Island: Dodger Channel, Barkley Sound; mature male and female from the collection of D. Zittin, 1976.

**Distribution:** Queen Charlotte Islands, B.C. (53°15'N, 132°00'W), south to Santa Barbara, California (34°N, 120°W).

**Ecology:** Occurs amongst kelp holdfasts on high salinity exposed coasts, intertidally in the north and subtidally to 17 m in the south.

**Diagnosis:** Body slender. Antenna 1 peduncle 1

lacking a ventral distal spine. Antenna 2 long and slender,  $\frac{1}{3}$  to  $\frac{3}{4}$  length of antenna 1; flagellum weakly setose, proximal 2-4 segments fused. Gnathopod 1 dactyl overlapping the palm by only about the length of the nail. Gnathopod 2 (♀), lower lobe of segment 5 rounded. Gnathopod 2 (♂), hand rectangular, dactyl sinuous, increasing with age to the full length of the hand; palm smooth, with a low, rounded process near the dactyl hinge. Peraeopod 5, lower hind edge of segment 2 convex, evenly rounded. Peraeopods 6 and 7 weakly setose, segment 2 slender, margins parallel. Uropods 1 and 2, rami slender. Body length at maturity: Male 7-10 mm, female 7.5-12.5 mm.

**Remarks:** The individuals described here differ

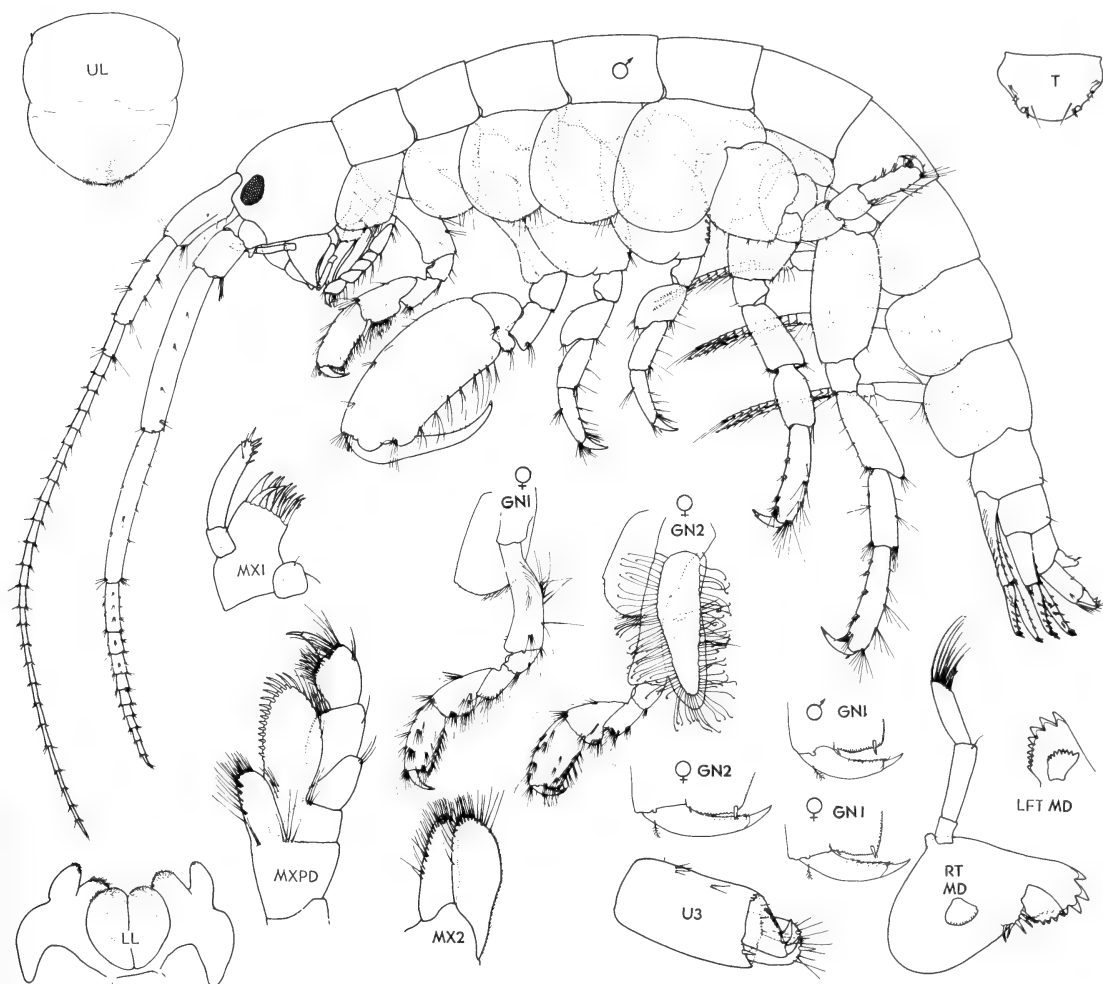


Figure 15. *Peramphithoe plea* (Barnard) ♂ 10.0 mm; ♀ 12.5 mm, Dodger Channel, Barkley Sound, Vancouver Is., B.C. 28 June 1976. Queen Charlotte Is., B.C. 19 August 1957

slightly from Barnard's holotype in that antenna 2 flagellum is less setose, the dactyl of gnathopod 1 is somewhat longer and the dactyl of the male gnathopod 2, although of a specimen 1.5 mm longer than the holotype, does not reach the full length of the hand.

The two species from the boreal coast of South America warrant inclusion in the monograph because their morphology verifies conclusions justifying the transfer of the transverse-handed *Ampithoe* to the new genus *Peramphithoe*. They meet all diagnostic criteria for the genus and most closely resemble members of the *P. lindbergi* group. The first appears to be, from the descriptions of Stebbing (1906) and Kreibohm de

Paternoster & Escofet (1976), *Ampithoe femorata* Krøyer 1845 (herein re-described and assigned the new generic title). The second is a new species found in colonies amongst the fronds of *Lessonia* in self-constructed chambers (H.K. Schminke, pers. comm.). It is consequently assigned the name *Peramphithoe lessoniophila*.

***Peramphithoe femorata* (Krøyer 1845)**

Figure 16.

*Ampithoe femorata* Krøyer 1845, p. 335, figs. 4a-i

*Ampithoe femorata*: Stebbing, 1906, p. 636-637; Chilton, 1921, p. 88; Schellenberg, 1931, p. 245; Kreibohm de Paternoster & Escofet,

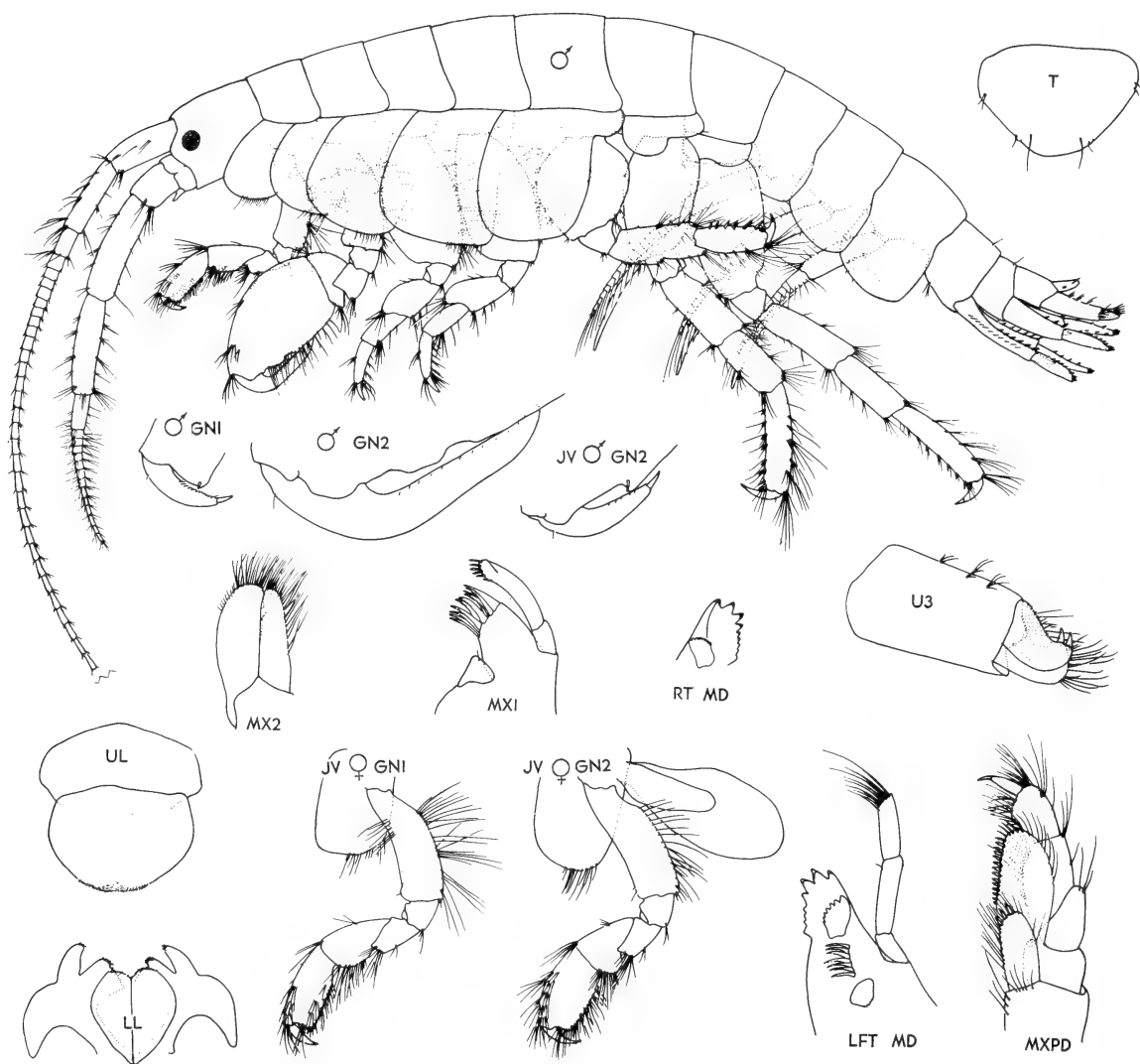


Figure 16. *Peramphithoe femorata* (Krøyer) ♂ 18.0 mm; ♂ subadult 12.5 mm; ♀ subadult 13.0 mm. Cape Horn Is., South America. 1970.

1976, p. 77-91, figs. 1-3; (not J.L. Barnard, 1952, p. 24-28, pls. 6-7); Alonso, 1980, p. 4-5, fig. 1.

? *Amphithoe gaudichaudii* H. Milne Edwards 1840, p. 31

*Amphithoe brevipes* Dana 1852, p. 216; 1853-55, p. 941, pl. 64, figs. 5a-n.

*Ampithoe brevipes*: Stebbing, 1906, p. 637; 1914, p. 371, ? K.H. Barnard, 1916, p. 255-256, fig. 34.

? *Amphithoe peregrina* Dana 1853-55, p. 940, pl. 64, figs. 4a-b; 1862, p. 247, pl. 43, fig. 1

? *Amphithoe falklandi* Bate 1862, pp. 237-248, figs. 1, 2, 6.

? *Amphithoe rubricata*: Della Valle, 1893, p. 456, 459 (not Montagu 1808)

? *Grubia crassicornis*: Della Valle, 1893, p. 456

**Material examined:** Cape Horn Island, South America (55°S, 77°W), 1970 stn. 27896, J. Markham collector, 1 adult ♂, 1 subadult ♂, 1 subadult ♀, 1 immature; Banco de los Tacas, Isla Navarino, South Chile (55°05'S, 67°04'W), 5 February 1970, stn. 27924, J. Markham collector, 9.5°C, 2 subadult ♂♂.

**Distribution:** New Zealand, South Africa, Chile, Argentina, Brazil?

**Ecology:** No sampling data available. Kreibohm de Paternoster and Escofet (1976) found the species in tubes rolled in the fronds of *Macrocystis pyrifera*.

**Diagnosis:** Body relatively stout, eye medium. Antenna 1 long, about  $\frac{1}{2}$  body length; peduncle segment 1 without a posterodistal spine. Antenna 2 stout, about  $\frac{1}{2}$  length of antenna 1, flagellum strongly setose, proximal segments of flagellum fused. Lower lip outer lobes, apical subequal to medial. Gnathopod 1, segment 5 somewhat shorter than 6, dactyl overlapping the palm by considerably more than the length of the nail. Gnathopod 2 (♂), hand enlarged, palm crenulated, nearly straight, bearing a tubercle; dactyl sinuous, reaching to  $\frac{2}{3}$  the length of the hand; in the juvenile (10.5 mm and 12.5 mm), palm slightly concave, not crenulated, tubercle absent; dactyl evenly curved,  $\frac{1}{3}$  -  $\frac{1}{2}$  length of the hand. Gnathopod 2 (♀) segment 5 shorter than 6 and narrowed into a posterior lobe; segment 6 similar in form to, but broader than segment 6 of gnathopod 1. Peraeopods 3 and 4, segment 4 strongly overhanging segment 5. Peraeopod 5, lower hind edge of segment 2 evenly curved or slightly concave; segment 4 slightly longer than 5. Peraeopods 6 and 7 moderately

setose, segment 2 proximally broadened. Uropods 1 and 2 slender. Body length reaching 22 mm.

### *Peramphithoe lessoniophila* n.sp.

Figure 17.

**Material examined:** Near Coquimbo, Chile (30°S, 71°W). A. Viviani, collector. Holotype ♂ (NMC-C-1981-964); allotype ♀ (NMC-C-1981-965); paratypes (NMC-C-1981-966).

Smithsonian collections (USNM): 1 ♂, 1 ♀.

**Ecology:** Found living in little chambers self-constructed in the fronds of *Lessonia* (H.K. Schminke, pers. comm.)

**Description of male holotype**, 9.5 mm: Body stout, eye medium. Antenna 1 short, less than  $\frac{1}{2}$  the body length; peduncle segment 1 without a posterodistal spine. Antenna 2 about  $\frac{3}{4}$  the length of antenna 1, flagellum strongly setose, proximal segments of flagellum fused. Lower lip outer lobes, apical longer than medial. Gnathopod 1, segment 5 subequal to 6, dactyl overlapping the palm by more than the length of the nail. Gnathopod 2, hand enlarged, palm smoothly concave; dactyl evenly curved, reaching to  $\frac{1}{2}$  the length of the hand. Peraeopods 3 and 4, segment 4 strongly overhanging segment 5. Peraeopod 5, lower hind edge of segment 2 concave; segment 4 slightly longer than 5. Peraeopods 6 and 7 moderately setose, segment 2 proximally broadened. Uropods 1 and 2 slender. Body length: male 9.5 mm, female 7-8.5 mm.

**Description of female allotype**, 7 mm: Gnathopod 1 as in the male. Gnathopod 2, segment 5 shorter than 6 and narrowed into a posterior lobe; segment 6 similar in form to, but broader than segment 6 of gnathopod 1. Appendages otherwise as in the male.

**Etymology:** "*Lessonia* - loving", referring to the construction of tubes in the fronds of the kelp *Lessonia*.

## Discussion and Conclusions

### *Biogeography and Ecology*

Tables 2 and 3 summarize the geographic and ecological distributions of the northern Pacific Ampithoidae. The species are divisible into the following groups:

1. Pan-Pacific, cold water species further subdivisible into
  - a) subarctic species *Ampithoe volki*, *Peramphithoe mea*, and
  - b) subarctic and boreal species *Ampithoe*

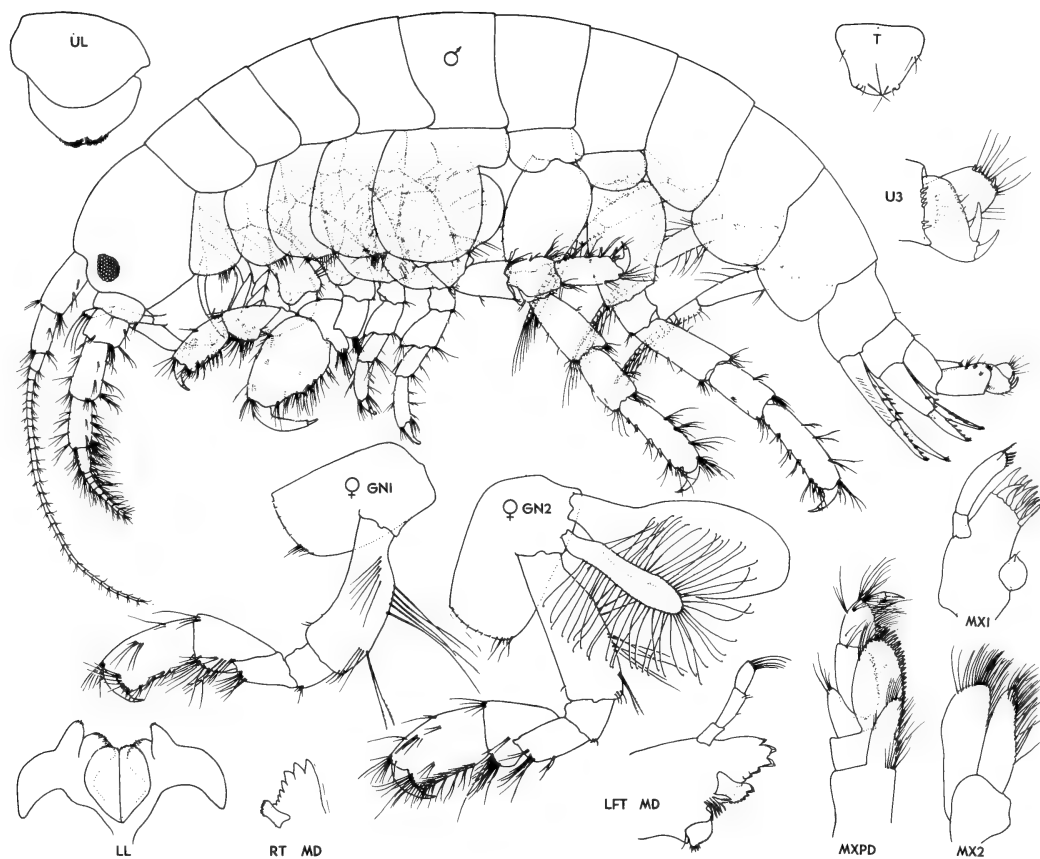


Figure 17. *Peramphithoe lessoniophila* n.sp. ♂ 9.5 mm; ♀ 7.0 mm. Near Coquimbo, Chile

*kussakini*, *A. lacertosa* and *P. lindbergi*, these occurring in a broader range from Alaska to California. The species generally occur in high salinity exposed and semi-protected coasts although *A. lacertosa*, having the broadest geographical and ecological range, occurs also in lower salinity protected embayments and estuaries.

2. Aleutian-endemic, subarctic species *Ampithoe rubricatoides* occurring in high salinity cold waters.
3. American-endemic, boreal species *Cymadusa uncinata*, *Ampithoe sectimanus*, *A. dalli*, *A. simulans*, *P. humeralis*, *P. tea* and *P. plea* occurring variously from southern Alaska to California in exposed and semi-protected meso- and polyhaline waters.
4. American-endemic, primarily warm water species *Ampithoe valida* and *A. plumulosa*.

These occur south of central British Columbia. *A. valida* occurs also in the Atlantic and is restricted to low salinity protected coasts.

All species occur amongst algae and debris in tide-pools, the intertidal and subtidal coast, to the limits of the photic zone. Greatest diversity in the northeastern Pacific is achieved in the environs of Vancouver Island (12 species). Seven species occur as far north as the Aleutian Islands of Alaska and probably beyond.

#### Taxonomic Considerations

Table 4 shows that there are many differences between the northeastern Pacific *Cymadusa*, *Ampithoe* and *Peramphithoe* which, on further investigation by Conlan (in press) prove to be universal. All three genera are wide ranging in both hemispheres, although *Cymadusa* and *Ampithoe* concentrate in the tropics while



*Peramphithoe* predominates in boreal waters. The more apomorphic *Peramphithoe* is less diverse, and morphologically less variable than the more plesiomorphic *Cymadusa* and *Ampithoe*. This is demonstrated by the two South American species of *Peramphithoe* which little differ from the North American species. The alteration in palm configuration in *Peramphithoe*, coincident with strong development of the peraeopod spinning glands and uropod spinous processes must incur a measurable change in living and tube-building habits. An examination of the evolutionary relationships of these genera with other Amphithoidae is presented separately (Conlan, in press).

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**Table 1. Comparative characters of the North American and type (USSR) specimen of *Ampithoe volki***

Character	Type specimen (as published) Gurjanova 1938	North American Specimens
Size at maturity	≤ 6 mm	> 8 mm (♀ not ovigerous at this size)
Antenna 1 — length	1 slightly > 2	1 slightly to markedly < 2
flagellum	17-22 segments	14 segments
Lower lip	apical ≈ medial	apical > medial
Maxilla 1 inner plate	lacking setae	bearing 1 seta
Maxilliped palp	segment 3 = segment 2	segment 3 < 2
Gnathopod 2 ♂	thumb triangular	thumb square (but not appearing to have been broken)
	segment 2 not lobate	segment 2 lobate
Epimeron 3 ♂	posterodistal angle forms an extended denticle	posterodistal margin smoothly angled
Uropod 3 — peduncle	stout, nearly as wide as long	slender, length 1-1/3 times the width
outer ramus	bearing a central spine	lacking a central spine

**Table 2. Distribution of Northeastern Pacific Ampithoidae listed in geographic order**

Species	Northern					Washington	Oregon	California	Other Records
	Aleutian Is., Alaska	Prince William Sound Alaska	Cross Sd. to Dixon Entrance Alaska	B.C. and Queen Charlotte Is. B.C.	Central B.C. and Vancouver				
<i>Peramphithoe mea</i>	X	—	—	—	—	—	—	—	USSR: Japan Sea
<i>Ampithoe rubricatoides</i>	X	—	—	—	—	—	—	—	
<i>Ampithoe volki</i>	X	—	—	—	—	—	—	—	USSR: Japan Sea
<i>Ampithoe kussakini</i>	X	X	X	X	O	—	—	—	Preobrazhen'e Bay USSR: Shikotan Is. (Otradnaya Bay)
<i>Ampithoe dalli</i>	X	X	X	X	X	X	X	—	
<i>Ampithoe simulans</i>	X	X	X	X	X	X	X	—	
<i>Ampithoe lacertosa</i>	O	X	X	X	X	X	X	X	Japan: Schizueka Prefecture
<i>Ampithoe sectimanus</i>	—	X	X	X	X	—	X	—	
<i>Peramphithoe humeralis</i>	—	X	X	X	X	X	X	X	
<i>Peramphithoe lindbergi</i>	—	X	X	X	X	X	X	X	USSR: Bering Sea, Okhotsk Sea, Japan Sea
<i>Peramphithoe tea</i>	—	X	X	X	X	X	X	X	
<i>Cymadusa uncinata</i>	—	—	O	O	X	O	—	X	
<i>Peramphithoe plea</i>	—	—	—	X	X	X	X	X	
<i>Ampithoe valida</i>	—	—	—	—	X	X	X	X	Japan, US mid Atlantic coast
<i>Ampithoe plumulosa</i>	—	—	—	—	O	—	—	X	Mexico, Ecuador, Galapagos Is.
Number of species	7	8	9	10	12	9	9	8	

X abundant, O occasional, — absent

Table 3. Habitats of Northeastern Pacific Amphithoidae

Species	Coastal Exposure		Salinity Range				Depth Range		
	Open and semi-protected	Protected	Marine polyhaline (≥ 28‰)	Meso-haline (10-27‰)	Oligo-haline (1-9‰)	Fresh-water (< 1‰)	Subtidal	LW-MW	MW-HW
<i>Peramphithoe mea</i>	X	—	X	—	—	—	to 60 m	0	?
<i>Ampithoe rubricatoides</i>	X	—	X	—	—	—	to 18 m	—	?
<i>Ampithoe volki</i>	X	—	X	—	—	—	to 15 m	X	in tidepools
<i>Ampithoe kussakini</i>	X	O	X	X	O	—	to 15 m	X	in tidepools
<i>Ampithoe dalli</i>	X	X	X	X	O	—	to 10 m	X	in tidepools
<i>Ampithoe simulans</i>	X	—	X	O	O	—	to 4 m	X	in tidepools
<i>Ampithoe lacertosa</i>	X	X	X	X	O	O	to 10 m	X	in tidepools
<i>Ampithoe sectimanus</i>	X	—	X	O	—	—	to 3 m	X	in tidepools
<i>Peramphithoe humeralis</i>	X	O	X	O	—	—	to 70 m	X	in tidepools
<i>Peramphithoe lindbergi</i>	X	O	X	O	—	—	to 18 m	X	in tidepools
<i>Peramphithoe tea</i>	X	O	X	O	—	—	to 67 m	X	in tidepools
<i>Cymadusa uncinata</i>	X	O	X	—	—	—	to 7 m	X	in tidepools
<i>Peramphithoe plea</i>	X	—	X	—	—	—	to 17 m	X	in tidepools
<i>Ampithoe valida</i>	O	X	O	X	X	—	to 32 m	X	in tidepools
<i>Ampithoe plumulosa</i>	NO DATA						to 75 m	X	in tidepools

X abundant, O occasional, — absent

Table 4. Character differences in the Northeastern Pacific *Cymadusa*, *Ampithoe* and *Peramphithoe*

Character	<i>Cymadusa</i> Savigny	<i>Ampithoe</i> (Leach)	<i>Peramphithoe</i> n.gen
Antenna 1, accessory flagellum	multisegmented	vestigial	absent
Mandible,			
incisor, no. teeth	7	5-9	6-17
lacinia mobilis, no. teeth	5-6	4-7	6-17
no. spines	6-10	5-9	6-14
palp setosity	strong	moderate to strong	weak
Maxilla 1,			
inner plate, no. setae	3	0-1	1
palp, no. spines	10	5-12	4-8
no. setae	5	3-7	1-4
Maxilliped,			
outer plate, inner margin	smooth	fringed	smooth
teeth	smooth	usually smooth	serrated
Gnathopod 1,			
sexual dimorphism	absent	present	absent
obturator spine	strong	strong	weak
coxa produced forward	yes	yes	no
Coxae 1-5,			
lower margin setose	yes	rarely	always
Peraeopods 3 and 4,			
segment 2	weakly inflated	weakly inflated	strongly inflated
segment 4	moderately inflated	moderately inflated	strongly inflated
Pleopods,			
no. coupling hooks	5-6	6-11	4-8
Uropod 1,			
spinous peduncular process	well developed	vestigial or absent	well developed
Uropod 3,			
no. peduncular marginal spines	11	0-13	1-6
outer ramus serrations	weak	weak	strong
uncini	medium	medium	strong
Telson,			
no. setae at cusp	many	1-many	1
No. species	1	12	5
Percentage of total	10	24	36



# The Superfamily Corophioidea in the North Pacific Region. Family Aoridae: Systematics and Distributional Ecology

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## ABSTRACT

Amphipod crustaceans of the corophioidean family Aoridae were studied in extensive collections from the northeastern Pacific coastal marine region. Redefined herewith is the genus *Aoroides* Walker and the species *A. columbiae* Walker, *Lembos* (*Lembos*) *concavus* Stout and *Lembos* (*Arctolembos*) *arcticus* (Hansen). Newly described are *Columbaora* new genus and *C. cyclocoxa* new species, *Aoroides inermis* new species, *A. intermedius* new species, *A. exilis* new species, and *A. spinosus* new species. The geographic range of *Lembos* (*Lembos*) *concavus* Stout is extended north from California to British Columbia and of *Lembos* (*Arctolembos*) *arcticus* east to the Bering Sea. A key to recorded and probable species of Aoridae of the northeastern Pacific region is provided and phyletic relationships are examined. Of the boreal merochelate Aoridae, *Columbaora* is hypothesized to be closest to the ancestral form, from which separately evolved *Aora* and *Aoroides*.

## RÉSUMÉ

Les auteurs ont étudié les Crustacés amphipodes corophioïdés de la famille des Aoridae qui se trouvent réunis dans d'importantes collections provenant des eaux côtières du nord-est du Pacifique. Le genre *Aoroides* Walker et les espèces *A. columbiae* Walker, *Lembos* (*Lembos*) *concavus* Stout et *Lembos* (*Arctolembos*) *arcticus* (Hansen) sont redéfinis. Le nouveau genre *Columbaora* et les nouvelles espèces *C. cyclocoxa*, *Aoroides inermis*, *A. intermedius*, *A. exilis* et *A. spinosus* sont décrits pour la première fois. Les auteurs ont étendu l'aire de répartition de *Lembos* (*Lembos*) *concavus* Stout vers le nord depuis la Californie jusqu'à la Colombie-Britannique, et celle de *Lembos* (*Arctolembos*) *arcticus* vers l'est jusqu'à la mer de Béring. Une clé des espèces signalées et probables d'Aoridés du nord-est du Pacifique apparaît et les auteurs examinent les relations phylétiques. Ils formulent l'hypothèse que, parmi les Aoridés mérochéliformes de l'hémisphère boréal, *Columbaora* serait la forme la plus rapprochée de l'ancêtre dont auraient évolué séparément le genre endémique du Pacifique, *Aoroides*, et le genre endémique de l'Atlantique, *Aora*.

## Introduction

The family Aoridae encompasses a diverse group of tube-building corophioidean amphipods that is diagnosed by a combination of morphological features, rather than by any single character. Myers (1969 p. 95) described the family as those members of the Corophioidea "which exhibit greater development of gnathopod 1 than gnathopod 2, coupled with a tendency towards retention of such primitive characters as an accessory flagellum on the antennule, uropod 3 with two rami, contiguous coxae, and no marked depression of the pleon." Barnard (1973) proposed to combine the Aoridae, along with the

Isaeidae and Photidae into the Corophiidae, producing a large family of diverse origins. Bousfield (1973) and (1982) and Myers (1981) have retained Aoridae as a separate family and expanded the concept to include several convergently depressed-bodied genera such as *Unciola*, *Pseudunciola* and *Rildardanus*. The separate family concept is maintained in this study.

Of the 38 genera and more than 100 species currently included in the family Aoridae, only one species, *Aoroides columbiae* Walker 1898, had previously been recorded from boreal eastern

Pacific waters. A second species, *A. californica* Alderman 1936, had been synonymised with *A. columbiae* by Barnard (1954). Apart from the records of Thorsteinson (1941), no other illustrated documentation has been made of the Aoridae from the east Pacific north of 48° latitude. This report attempts to fill the distributional hiatus and clarify the attendant taxonomic problems through examination of more than 6,000 specimens of Aoridae acquired by the National Museum of Natural Sciences and many individual collectors from Oregon to the Aleutian Islands of Alaska. Station data are recorded in Bousfield (1957, 1963) Bousfield and McAllister (1962) and Bousfield (1968) for expeditions to Vancouver Island and Georgia Strait, B.C., Queen Charlotte Islands, the southern Alaska coast and the north and central British Columbia coast, respectively. Station data for 1966 (Washington and Oregon), for 1970, 1975 to 1977 (Vancouver Island and southern British Columbia mainland coast) and 1980 (southern Alaska coast) are provided in Bousfield & Jarrett (1981).

In order to facilitate identification the keys and descriptions are constructed with sex and age independent characters, except where stated. In addition, information on pigmentation patterns is provided. These pigments should remain in alcohol-preserved specimens for up to 10 years. Table 5 lists the locality of specimens deposited in the Smithsonian Institution (USNM) and the Zoological Museum, Leningrad, USSR.

## SYSTEMATIC SECTION

### Family Aoridae Stebbing 1899

Barnard, J.L. (1969), p. 147

Myers, A.A. (1981), p. 9, 10

Bousfield (1973, p. 165 1979, 1982, p. 284)

Body smooth, slender, often depressed or broadened. Colour pattern characteristically disruptive. Mid-sternal spines or bulges occasionally present; pleon and urosome occasionally sparsely setose dorsally, segments rarely coalesced. Head shallow, rostrum generally absent or short. Eyes small, rounded, or lacking. Interantennal head lobe not pronounced. Antennae slender to stout, 1 usually the longer; inferior antennal sinus shallow; peduncles long, moderately spinose or setose, that of 2 often stout or incrassate in ♂; accessory flagellum multi-

articulate, short or vestigial, rarely lacking. Upper lip rounded below, epistome not produced. Mandible, molar strong; palp slender, segment 3 normally setose. Lower lip, mandibular lobes often elongate. Maxilla 1, inner plates setose or bare; outer plate usually with 10 apical spine-teeth; palp large. Maxilla 2, normal, inner plate bearing facial setae. Maxilliped, plates strong; palp medium.

Coxae 1-4 medium deep to very shallow, weakly overlapping or not contiguous; coxa 1 often produced forward. Gnathopod 1 larger than gnathopod 2, subchelate or, in the male, often carpochele or merochele. Gnathopod 2 subchelate, segments 5 and 6 slender. Peraeopods 3 and 4 weakly glandular, basis not expanded. Peraeopods 5-7 unequal, 7 longest, bases usually differently expanded; coxa 5 shallower than coxa 4. Pleopods normal, peduncle slender. Abdominal sideplates shallow, weakly overlapping or separated distally. Uropods 1 and 2 occasionally unequally biramous or uniramous, postero-distal peduncular spinous process usually present. Uropod 3 biramous or uniramous, outer ramus occasionally minutely 2-segmented; apices with simple spines lacking uncini. Telson entire, fleshy with small dorsal subapical cusps. Coxal gills sac-like, present on peraeopods 2-6. Brood plates large, laminar; marginal setae simple.

The family now contains nearly 180 species in 38 genera. Size is generally small (2-12 mm) but the deep water *Neohela* and the northern species *Lembos* (*Arctolembos*) *arcticus* (Hansen) reach 30 mm. Most species are shallow marine and estuarine and occur occasionally in tidal (rarely supratidal) freshwaters; a few are bathyal and abyssal. Diversity is greatest in tropical and warm-temperate regions of the northern hemisphere. Most members of the Aoridae are tube builders but some species crawl freely on the sea bottom and among sponges or occupy scaphopod shells or tubes of other animals.

On the northeastern Pacific coast (northern Alaska to northern California) the following species are herewith recorded: *Aoroides columbiae* Walker 1898, *A. exilis* n.sp., *A. inermis* n.sp., *A. intermedius* n.sp., *A. spinosus* n.sp., *Columbaora cyclocoxa* n. gen., n.sp., *Lembos* (*Lembos*) *concavus* Stout 1913 and *Lembos* (*Arctolembos*) *arcticus* (Hansen 1887). *Aoroides secunda* Gurjanova 1938 could conceivably occur in the northern regions of the northeastern Pacific; species in the southern limits might include



*Acuminodeutopus heteruropus* Barnard 1959,  
*Amphideutopus oculatus* Barnard 1959, *Lembos*  
*(Lembos) audbettius* Barnard 1962, *L.(L.) macro-*  
*manus* (Shoemaker 1925), *Microdeutopus schmitti*

Shoemaker 1942, *Neohela pacifica* Gurjanova  
 1953, *Neomegamphopus roosevelti* Shoemaker  
 1942, *Rildardanus tros* Barnard, and *Rudilemboides*  
*stenopropodus* Barnard 1959.

#### Key to Genera of the Aoridae of the Northeastern Pacific (Alaska to California)

1. Uropods 1 and 2, inner rami vestigial ..... *Rildardanus* Barnard  
 Uropods 1 and 2, inner rami well developed ..... 2
2. Uropod 3, inner ramus absent ..... *Neohela* Smith  
 Uropod 3, inner ramus short and scale-like or fully developed ..... 3
3. Head lobe acutely produced ..... 4  
 Head lobe rounded or bilobed ..... 6
4. Uropod 3, inner ramus less than half the length of the outer ..... *Acuminodeutopus* Barnard  
 Uropod 3, inner ramus more than half the length of the outer ..... 5
5. Antenna 1 segment 3 as long as segment 1. Mandibular palp segment 3 subclavate.  
 Gnathopod 1 (♂) carpochele ..... *Neomegamphopus* Shoemaker  
 Antenna 1 segment 3 shorter than segment 1. Mandibular palp segment 3 slender, elongate.  
 Gnathopod 1 (♂) usually carpochele ..... *Rudilemboides* Barnard
6. Antenna 1, accessory flagellum minute, vestigial. Mandibular palp slender, segment 3  
 cylindrical and weakly setose. Gnathopod 2 (♂) merochele, coxa rectangularly elongate  
 ..... *Aoroides* Walker (page 85)  
 Antenna 1 accessory flagellum multisegmented. Mandibular palp well developed, segment 3  
 more or less falcate and strongly setose. Gnathopod 2 (♂) usually carpochele or subchele  
 but if merochele, coxa circularly enlarged ..... 7
7. Gnathopod 1 (♂) carpochele. Gnathopod 1 (♀) segment 5 wider than 6, posterodistal  
 corner toothed ..... *Microdeutopus* Costa  
 Gnathopod 1 (♂) not carpochele. Gnathopod 1 (♀) segment 5 not wider than 6, postero-  
 distal corner not toothed ..... 8
8. Pleon lacking a pair of setae on the dorsum. Gnathopod 1 (♂) merochele, segment 5 much  
 longer than 6; coxa 1 (♂) circularly enlarged. Gnathopod 1 (♀), segment 5 subequal to 6;  
 segment 6 slender, distally tapered ..... *Columbaora* n. gen. (page 83)  
 Pleon with a pair of setae on the dorsum of at least one segment. Gnathopod 1 (♂) subchele,  
 segment 5 shorter than 6; coxa 1 (♂) not circularly enlarged. Gnathopod 1 (♀), segment 5  
 shorter than 6; segment 6 distally broadened ..... *Lembos* Bate (page 80)

#### Key to North Pacific Species of *Aoroides*

1. Uropod 2, peduncle lacking antero-distal spinous process ..... 2  
 Uropod 2, peduncle with antero-distal process well developed ..... 3
2. Gnathopod 1 (♂), anterior margin of segments 2 and 5 bearing dense plumose setae;  
 gnathopod 1 (♀), segment 2 lacking anterodistal group of setae .....  
 ..... *Aoroides secundus* Gurjanova 1938  
 Gnathopod 1 (♂), anterior margin of segments 2 and 5 bearing a few simple setae only;  
 gnathopod 1 (♀), segment 2 with well developed anterodistal group of setae .....  
 ..... *Aoroides nahili* J.L. Barnard 1970
3. Uropod 3 outer ramus usually bare, rarely with 1-2 small spines. Mandibular palp, segment 2  
 setose. Gnathopod 2, both sexes, palm slightly oblique, dactyl overlapping by more than the  
 length of the nail; segment 2 of the female with a group of long setae on the distal anterior  
 margin. Male gnathopod 1, hind margin of segment 2 bare ..... 4

- Uropod 3 outer ramus with 1-3 strong spines. Mandibular palp, segment 2 bare. Gnathopod 2, both sexes, palm transverse, dactyl overlapping by only the length of the nail; segment 2 of the female without group of long setae. Male gnathopod 1, hind margin of segment 2 setose . . . . . 6
4. Body pigmented in broad bands, parts of the head, segments 6 and 7 bare, giving a "saddle-back" appearance. Maxilliped outer plate, teeth strongly serrated, lower teeth with at least 1-4 cusps each. Gnathopod 1 (♂), segment 5 broader than segment 2, dorsal margin of 5 bare except for one distal group of short setae . . . . . *A. columbiae* Walker 1898 (page 89)  
Body pigmented in discrete speckles throughout. Maxilliped outer plate, lower teeth with 0-2 cusps each. Gnathopod 1, (♂), segment 5 not broader than segment 2, dorsal margin of 5 setose . . . . . 5
5. Body pigment (speckles) never concentrated in the lower hind corners of body plates 1-5. Maxilliped outer plate, teeth cusped. Gnathopod 1 (♂), dorsal margin of segment 5 with 5-7 bundles of setae . . . . . *A. intermedius* n.sp. (page 87)  
Body pigment (speckles) usually concentrated in the lower hind corners of body plates 1-5. Maxilliped outer plate, all mid to lower teeth smooth. Gnathopod 1 (♂), dorsal margin of segment 5 with 8-15 bundles of setae . . . . . *A. inermis* n.sp. (page 86)
6. Body pigmented in broad bands, parts of the head, segments 6 and 7 bare, giving a "saddle-back" appearance. Peraeopod 7 segment 2 slender (width/length = 39%). Gnathopod 1 (♂), segments 2 and 3 densely setose, setae as long as the width of the segment . . . . . *A. exilis* n.sp. (page 92)  
. . . . . *A. exilis* n.sp. (page 92)  
Body diffusely speckled throughout. Peraeopod 7, segment 2 broad (width/length = 56%). Gnathopod 1 (♂), segments 2 and 3 weakly setose, setae shorter than the width of the segments . . . . . *A. spinosus* n. sp. (page 93)

**Genus *Lembos*** Bate 1857 — Barnard 1969, Myers 1981

**Subgenus *Arctolembos*** Myers 1981

**Diagnosis:** Anterior lateral cephalic lobes bilobed; maxilliped palp article 2 extending beyond the distal end of the outer plate for  $\frac{1}{3}$  its length; maxilla 1 outer plate with more than 10 spines; lower lip, outer plate, anterior margin broadly truncate.

**Type Species:** *Microdeutopus arcticus* Hansen 1887

***Lembos (Arctolembos) arcticus*** (Hansen 1887)

Figure 1.

*Microdeutopus arcticus* Hansen 1887, p. 231, pl. 22, fig. 3; Stebbing, 1894, p. 43.

*Autonoe arctica* Della Valle 1893, p. 406, pl. 56, figs. 35-36.

*Lembos arcticus*, Stebbing, 1895, p. 207; 1906, p. 595; Brügger, 1909, p. 39, pl. 3, figs. 22-28; Gurjanova, 1951, p. 836, fig. 586 (part-figures on extreme right apply to *Proto-medeia grandimana* Brügger); Myers, 1981, pp. 269-273, figs. 200-202.

**Material examined:** Alaska — Bering Sea; 1 juvenile ♂, 1 subadult ♀ from St. Lawrence Island (64°N, 169°W). Slattery stn. 23, 33-38 m, 1 and 7 July 1980.

**Distribution:** Kara Sea (70°N, 63°E) (type

locality), Bering Sea (64°N, 169°W).

**Ecology:** An arctic species occurring subtidally on a sandy substratum.

**Diagnosis:** Male — Body with a pair of short setae on the dorsum of pleon segment 3 and urosome segment 1. Sternal processes absent. Head lobe shallow, bilobed. Coxal plates shallow, coxa 5 nearly as deep as coxa 4. Cuticle not especially shiny. Antenna 1 peduncle 1 with 4 ventral spines, accessory flagellum well developed, with up to 8 segments. Antenna 2, flagellum with up to 7 segments, first two the longest, terminal two segments distally spinose. Mandible with maximum 5 teeth and 8 raker spines; lacinia mobilis with maximum 4 teeth; palp strongly falcate, segment 2 with numerous inner marginal setae and two groups of outer setae; segment 3 subequal, inner margin strongly concave with a marginal row of long setae and in addition 4 groups each of long lateral and outer marginal setae; no seta at base of palp. Maxilla 1 inner plate with several minute setae; outer plate with up to 13 teeth; palp without setae at the base or on segment 1, 11 terminal spines and numerous lateral and marginal setae on segment 2. Maxilla 2 inner plate smaller than the outer. Maxilliped inner and outer plate teeth smooth and minute; palp segment 2 very long, extending beyond the distal end of the outer

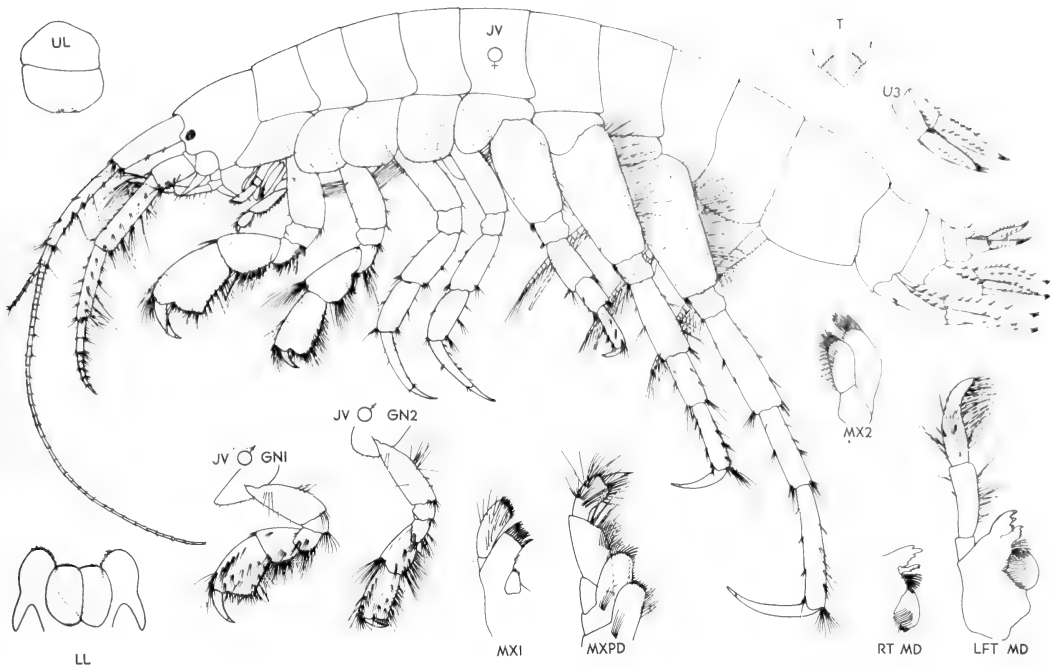


Figure 1. *Lembos (Arctolembos) arcticus* (Hansen) juvenile ♂ (16.0 mm), subadult ♀ (25.0 mm), St. Lawrence Is., Bering Sea. 1 and 7 July 1980

plate by about  $\frac{1}{3}$  its length; segment 3 without a distal protruberance, dactyl moderately large. Gnathopod 1, coxa 1 smaller and shallower than coxa 2, anterodistally produced; segment 2, anterior and lateral margins nearly bare, posterior margin with a group of long setae; segment 4 not prolonged into a long distal tooth; segment 5, posterior margin more than half the length of the anterior margin; segment 6 longer than 5, distally broadened, palm transverse and with a small defining tooth at the obturator spine (spine lacking in adult), dactyl not elongate, serrated in the juvenile, less so in the adult. Gnathopod 2, segment 2, anterior and lateral margins nearly bare, posterior margin with a group of long setae; segment 5 broadened distally, segment 6 slightly longer than 5, palm transverse; anterior margins of segments 5 and 6 not densely setose. Peraeopods 3 and 4, hind margin of segment 2 bearing a group of long setae; segment 5 not tapered proximally, slightly shorter than segment 4. Peraeopods 5-7, hind margin of segment 2, densely setose; no spine at posterodistal corner; dactyls progressively elon-

gated, from half the length of segment 6 in peraeopod 5 to four-fifths the length in peraeopod 7. Peraeopods 5 and 6, segment 5 lacking groups of comb spines. Peraeopod 7, segment 2 slender. Epimera 1-3, hind corner slightly notched, lateral ridge absent; lower margin of epimeron 2 not setose. Uropod spines strong; peduncular process of uropods 1 and 2 nearly half the length of the longest ramus. Uropod 2, inner ramus sinuous. Uropod 3, peduncle bearing lateral spines, lateral setae and terminal setae; inner ramus bearing lateral spines and terminal setae. Telson, each dorso-lateral crest with a group of 7-9 setae and a small apical cusp; posteroventral portion acutely produced. Gills short, plate-like.

Female. Coxa 1 not shallower than coxa 2; gnathopod 1, palm lacking a small tooth at the defining corner. Features otherwise as in the male.

Size range: male to 25 mm, female to 30 mm (not mature at 23 mm).

*Remarks:* This is a primitive aorid, as evidenced by the multi-segmented accessory flagellum of

antenna 1, well developed falcate mandibular palp, larger number of mandibular raker spines, well developed maxilla 1 palp, unaltered segments 4 and 5 of pereopods 3 and 4, well developed peduncular spinous process of uropods 1 and 2 and small, plate-like gills. It appears to have a number of features in common with *Leptocheirus* and *Protomedea* (Table 1) and in addition, many features not common to its genus. As such, full generic status may be justified, in recognition of its apparent transitional importance in linkage with the Isaecidae (Photidae).

#### Subgenus *Lembos* Myers 1981

**Diagnosis:** Anterior lateral cephalic lobes not bilobed; maxilliped palp segment 2 not extending beyond the distal end of the outer plate; maxilla 1, outer plate with 10 spines; lower lip, outer plate, anterior margin rounded.

**Type species:** *Lembos (Lembos) websteri* Bate 1857

**Additional Species:** A series of recent papers by Myers (summarized in Myers, 1981) has

revealed numerous new species of *Lembos* in the Mediterranean and Caribbean regions, at least one group of which will probably require new subgeneric status (Myers, personal communication)

#### *Lembos (Lembos) concavus* Stout 1913?

Figure 2.

*Lembos concavus*, Stout 1913, p. 36-41;

Barnard, 1962, p. 7-9, fig. 2.

**Material examined:** British Columbia — northern mainland: Townsend Pt., St. John Harbour; 7 specimens from Bousfield 1964 stn., H53, (52°12'N, 128°29'W). Surf exposed bedrock, boulders, *Phyllospadix*, kelp, *Corallina*: LW-MW; temperature 14.2°C, salinity 30.3‰. Vancouver Island: Sea Otter Cove; 3 specimens from Bousfield 1959 stn. O2B (50°40'N, 128°21'W). Dredge haul on stony bottom. Temperature 12.8°C, salinity 33.0‰.

**Distribution:** There is some uncertainty that these specimens are indeed *Lembos concavus* (see remarks below) and certainly this record is far north of its southern California habitat.

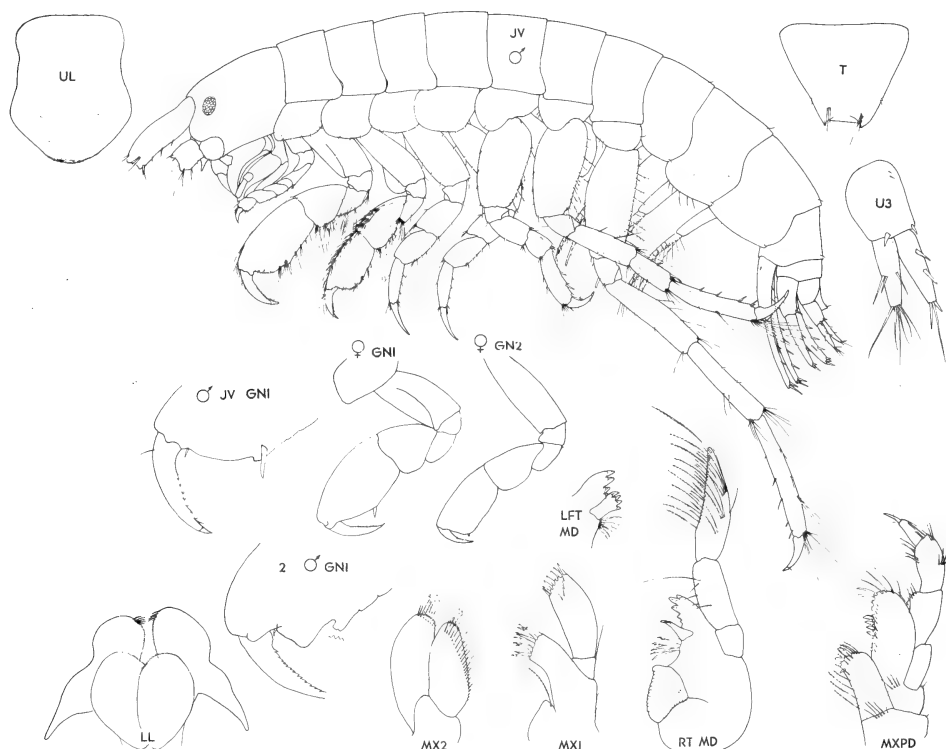


Figure 2. *Lembos (Lembos) concavus* Stout ♂ 4.0 mm, ♀ approx. 5 mm, mouth of San Josef Bay, Barkley Sound, Vancouver Is., B.C. 18 July 1959

*Ecology:* Temperate species living subtidally amongst algae.

*Diagnosis:* Male — Body with a pair of short setae on the dorsum of pleon segments 1-3 and urosome 1. Sternal processes absent. Head lobe medium, not bilobed; coxal plates shallow; coxa 5 as deep as coxa 4. Cuticle not especially shiny. Antenna 1 peduncle 1 with posterodistal spine; rest of antenna lost. Mandible with maximum 6 teeth and 6 raker spines; lacinia mobilis with maximum 4 teeth; palp falcate, segment 2 with 5 inner setae, and no outer setae, segment 3 the longer, inner margin convex with a marginal row of short comb setae, another of long setae plus several groups of lateral setae; no seta at base of palp. Maxilla 1 inner plate with 1 seta; outer plate with 10 teeth; palp with 2 setae at base, 1 seta on segment 1, 7 teeth and 4 setae on segment 2. Maxilla 2 inner plate nearly as broad as outer. Maxilliped inner and outer plate teeth smooth and well developed; palp segment 2 not extending beyond the distal end of the outer plate; segment 3 without a distal protruberance, dactyl moderately long. Gnathopod 1 subchelate, not elongate; coxa 1 neither enlarged nor shallower than 2 nor produced anteriorly; segment 2, margins nearly bare; segment 4 not prolonged into a long distal tooth; segment 5, posterior margin half the length of the anterior margin, not broadened distally; segment 6 longer than 5, palm transverse and with a small tooth at the obturator spine in the subadult, a larger square tooth proximal to the defining corner in the adult; dactyl not elongate, serrated. Gnathopod 2, segment 2, margins nearly bare; segment 5 not broadened distally; segment 6 as long as 5, anterior margins of each densely setose; palm transversely rounded. Peraeopods 3 and 4, hind margin of segment 2 bare; segment 5 tapered proximally, slightly shorter than segment 4. Peraeopods 5-7, hind margin of segment 2 moderately setose, lacking a spine at the posterodistal corner; dactyls barely increasing in length posteriorly. Peraeopods 5 and 6, segment 5 bearing two groups of comb spines. Peraeopod 7, segment 2 slender. Epimera 1-3, hind corner notched, lateral ridge present; lower margin of epimeron 2 setose. Uropod spines strong; peduncular process of uropods 1 and 2 nearly half the length of the longest ramus. Uropod 3, outer ramus with lateral setae, inner ramus laterally spinose and terminally setose. Telson

with a few setae at the apical cusps. Gills long, sac-like.

Female — Gnathopods barely sexually dimorphic. Gnathopod 1, palm apparently more oblique (see Barnard, 1962). Features otherwise as in the male.

Size range — male to 6 mm, female to 6 mm.

*Remarks:* There are some differences between these specimens and those of Barnard (1962) from southern California which may only be due to differences in age. In B.C. material, coxa 1 is not so acutely produced forward; the palm of the subadult male gnathopod 1 is oblique rather than transverse; segment 2 of gnathopod 2 is not antero-distally produced, margins are bare, the obturator spine is present, peraeopods 3 and 4 are much less densely setose and the lower margin of epimeron 2 is setose. The California male has a pair of setae on the dorsum of urosome 1 but in the B.C. specimens, pairs of dorsal setae are borne also on pleon segments 1, 2 and 3.

#### *Genus Columbaora* new genus

*Diagnosis:* Body with a pair of short setae on the dorsum of urosome 1. Segment 1 with a sternal hump or process. Head lobe strongly produced in the male, not bilobed. Coxal plates moderately deep, coxa 5 shallower than coxa 4. Antenna 1 accessory flagellum multi-segmented. Antenna 2 flagellum 6-7 segments, lower 3 segments distally spinose. Mandibular palp strong, falcate. Maxilla 1 inner plate with 1 seta; outer plate with 10 teeth. Maxilla 2 inner plate nearly as broad as outer. Maxilliped palp segment 2 not extending beyond the distal end of the outer plate; segment 3 with a distal protruberance, dactyl short. Gnathopods strongly sexually dimorphic. Male gnathopod 1 elongate, merochelate; segment 4 extending the full length of segments 5 and 6 together. Gnathopod 2, both sexes, subchelate, palm oblique, obturator spine small; segment 5 longer than 6, in the male becoming greatly elongate and densely setose. Peraeopods 3 and 4 slender, segment 5 slightly shorter than segment 4 and tapered proximally. Peraeopods 5-7, hind margin of segment 2 without long setae, lower hind corner not spinose, dactyls barely differing in length. Peraeopods 5 and 6, segment 5 with 3 groups of spines. Peraeopod 7, segment 2 with a broad hind lobe. Epimera 1-3, hind corner notched; lateral ridge present; lower margin of epimeron 2 setose.

Uropod spines moderately strong; peduncular process of uropods 1 and 2 long, more than half the length of the longest ramus. Uropod 3 both rami spinose and terminally setose. Telson with a few setae at the apical cusps. Gills long, sac-like.

*Type species: Columbaora cyclocoxa* new species.

*Etymology:* A compound word derived from British Columbia, the coastal region of most frequent occurrence and from *Aora* and *Aoroides* (in which the form of the first gnathopod (♂) is similarly merochelate).

*Relationship:* The first gnathopod of the male resembles that of *Aoroides* in the young, but diverges with age. Unlike *Aoroides* the second gnathopod is also strongly sexually dimorphic,

resembling that of the male *Lembos macromanus* (Shoemaker). *Columbaora* shows closer relationships with *Lembos* also in the form of the mandibular palp and in the possession of setae on the lower margin of epimeron 2.

***Columbaora cyclocoxa* n.sp.**

Figure 3.

*Type locality:* Klokachef Is., Chichagof Is., Alaska (57°25'N, 135°52'W). Bousfield and McAllister 1961 station A168, 24 July 1961. Under boulders and amongst *Laminaria* at low water. Temperature 12.0°C, salinity 30.9‰. Holotype ♂, NMC-C-1981-975; Allotype ♀, NMC-C-1981-958; Paratypes NMC-C-1981-959-960.

*Material examined:* Alaska — southern tip: 10

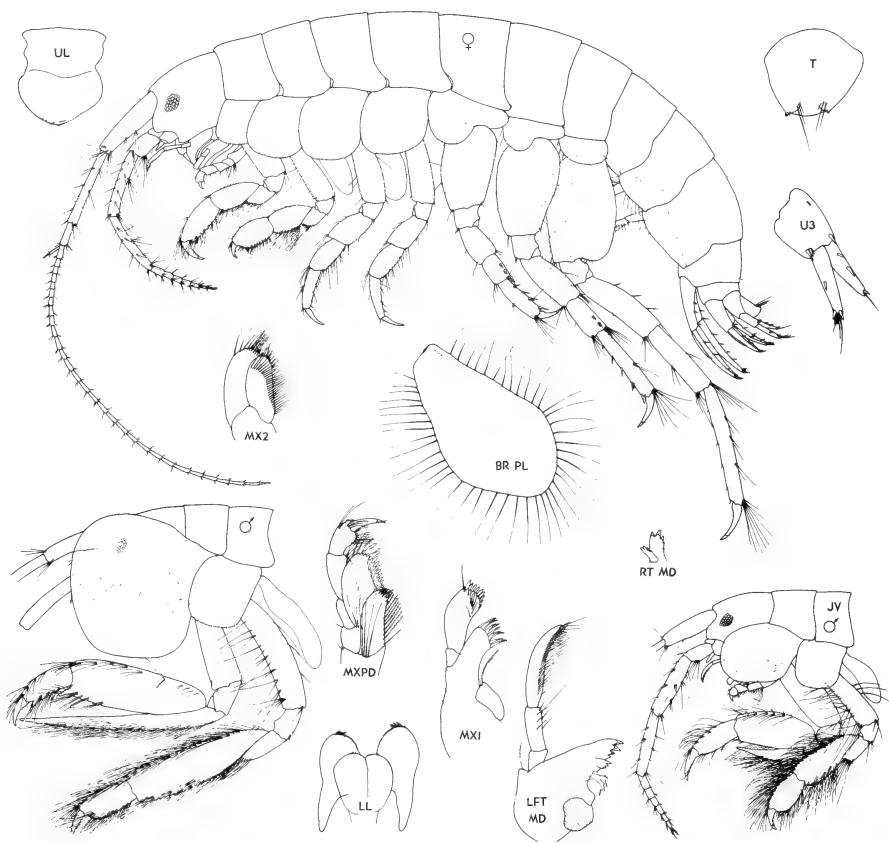


Figure 3. *Columbaora cyclocoxa* n. gen., n.sp. holotype ♂ 6.5 mm, allotype ♀ 7.0 mm, Klokachef Is., Chichagof Is., Alaska, 24 July 1961; paratype juvenile ♂ 4.0 mm, Codfish Pass, Miles Is., B.C. 5 August 1964

specimens from Bousfield and McAllister 1961 stns. A168, A171-2. British Columbia — northern mainland: 50 specimens from Bousfield 1964 stns., H5, H8, H30, H47 (paratype juvenile), H50, H65. Vancouver Island: 2 specimens from Bousfield 1977 stn. B6a; 1 specimen from Bousfield 1975 stn. P16b; 8 specimens from Bousfield 1970 stns. P709, P710, P715; 4 specimens from Bousfield 1959 stns. O26, V11. Washington: 3 specimens from Mukkaw Bay, Bousfield 1966 stn. W40.

**Distribution:** Chichagof Is., Alaska (57°25'N, 135°52'W) south to Mukkaw Bay, Washington (48°19'N, 124°40'W).

**Ecology:** Occurs amongst algae in the low intertidal and subtidally to 20 m depth on surf-exposed high salinity coasts. Summer temperatures 10-14°C, salinity 30.5-33.0‰. Female ovigerous in July and August.

**Diagnosis:** Male holotype (6.5 mm). Head lobe strongly produced with age. Cuticle very shiny. Antenna 1 peduncle with a posterodistal spine; accessory flagellum 1¼ segments. Mandible with maximum 6 teeth, 4 raker spines; lacinia mobilis with maximum 4 teeth; 1 seta at base of palp; segments 2 and 3, inner margins setose. Maxilla 1 palp with 3 setae at base, no setae on segment 1, maximum 9 teeth and 8 setae on segment 2. Maxilliped inner and outer plate teeth serrated and well developed. Coxa 1 circular, enlarging with age to enclose the head; gnathopod 1, segment 2 bare, segment 4 prolonged into a long distal tooth which extends with age beyond segment 6 to meet the dactyl; segment 5 elongate, in oldest specimens produced into a ventrodistal tooth; segment 6 shorter than 5, in old specimens produced at the location of the obturator spine into a ventrodistal tooth; dactyl not elongate, serrated in young, smooth in old; segments 2, 3 and dactyl without setae, segments 4, 5 and 6 strongly setose. Gnathopod 2, segment 2, anterior margin setose; segment 5 longer than 6, not broadened distally, but elongating with age and margins densely setose; segment 6, margins densely setose, palm oblique, obturator spine small; dactyl not overlapping the palm.

Female allotype (7.0 mm) — Head lobe moderately produced. Coxa 1 smaller and shallower than coxa 2; gnathopod 1 somewhat larger than gnathopod 2, subchelate; segment 5 subequal to segment 6, not posteriorly lobed; palm transverse, dactyl strongly overlapping. Gnathopod 2, segment 2, nearly bare; segment 5

slightly longer than segment 6, anterior margin bare; segment 6, anterior margin bare, palm oblique; dactyl not overlapping the palm. Features otherwise as in the male.

Size range: Male 4-6.5 mm, female 4-7 mm.

Pigmentation pattern: Brown bands on head and segments 1, 2, 4, 5 and 7.

**Etymology:** The species designation is descriptive of the large circular first coxa, distinctive in the male.

**Remarks:** In common with *Lembos* (*Lembos*) *concavus* and *Lembos* (*Arctolembos*) *arcticus*, the gnathopods of this species do not differ greatly in size. However, they exhibit considerable alteration from the normally subchelate form of the female. Primitive features are the presence of (albeit shorter) accessory flagellum, well developed mandibular palp and maxilla 1 palp. The shorter accessory flagellum, fewer mandibular raker spines, less setose maxilla 1 inner plate, altered segments 4 and 5 of pereopods 3 and 4 and long, plate-like gills suggest a more apomorphic form and a closer relationship to *Lembos* (*Lembos*) *concavus*.

By comparison with the merochelate genus *Aora* which occurs in the Indo-Pacific and Atlantic, *Columbaora* appears to be somewhat more primitive in the possession of a more falcate mandibular palp and well developed peduncular spinous process on both uropods 1 and 2. The greatly enlarged circular first coxa, more elongate fourth segment of the first gnathopod and greatly elongate fifth segment of the second gnathopod of the male is distinctive of the species.

#### Genus *Aoroides* Walker (revised)

Type species: *A. columbiae* Walker 1898

Additional northeastern Pacific species:

*A. inermis* new species

*A. intermedius* new species

*A. exilis* new species

*A. spinosus* new species

**Diagnosis:** Body with a pair of short setae on the dorsum of pleon 3 and urosome 1. Sternal bump or process on segment 1. Head lobe medium, not bilobed. Coxal plates shallow, coxa 5 as deep as coxa 4. Cuticle not especially shiny. Antenna 1, peduncle 1 lacking a ventrodistal spine; accessory flagellum minute, vestigial. Antenna 2, flagellum of 3½ segments, first much longer, each segment distally spinose. Mandibular palp slender, cylindrical, segment 2 with 0-2 setae, segment 3 slightly longer, inner



margin with 2-7 setae, no setae at base of palp. Maxilla 1 inner plate with 1 seta; outer plate with 10 teeth. Maxilla 2 inner plate much more slender than outer. Maxilliped inner plate teeth serrated, outer plate teeth serrated or smooth; palp segment 2 not extending beyond the distal end of the outer plate; palp segment 3 with a distal protruberance, dactyl short. Gnathopods strongly sexually dimorphic. Male gnathopod 1 elongate, merochelate; coxa elongating with age to mask laterally the buccal mass; segment 2, anterior, lateral and in some species, posterior margin setose; segment 4 prolonged into a long distal tooth extending to the junction of segments 5 and 6; segment 5 shorter than 6, as broad as 5 in young but slendering with age; never a distal tooth; dactyl serrated in young, losing cusps, elongating and bearing dense marginal setae at maturity; all segments moderately to densely setose. Gnathopod 2, both sexes, subchelate; segment 2, anterior margin setose, posterior margin bare; segment 5 subequal to 6, not broadened distally, margin not densely setose; segment 6, margins not densely setose, palm transverse, obturator spine normal, dactyl overlapping the palm. Peraeopods 3 and 4 slender, segment 5 longer than segment 4 and barely tapered proximally. Peraeopods 5-7, hind margin of segment 2 with or without long setae, lower hind corner marked by a long slender spine; dactyls barely differing in length. Peraeopods 5 and 6, segment 5 with 2 groups of spines. Peraeopod 7, segment 2 slender or moderately expanded. Epimera 1-3, hind corner notched, lateral ridge lacking; lower margin of epimeron 2 bare. Uropod spines slender; peduncular process of uropods 1 and 2 about  $\frac{1}{3}$  the length of the longer ramus. Uropod 3 rami with or without lateral spines, both rami terminally setose, outer more so than inner. Outer ramus 2-segmented, distal segment minute. Telson with a few setae at the apical cusps. Gills long, sac-like.

*Type species: Aoroides columbiae* Walker 1898.

Coloration: Basic body colour is white or orange, in some species alternating in bands on the antennae with red. Superimposed is a darker pigmentation in distinct speckles, concentrated spots or broad bands, the pattern which, except in recently moulted individuals, remains distinctive in alcohol for up to 10 years storage. Females brood up to 45 eggs. Young are released soon after hatching.

*Distribution:* Endemic to the north Pacific

region (Alaska to California); previous records from Hawaiian Islands, Pacific coast of USSR, and Japan await confirmation.

*Remarks:* The reduction of the accessory flagellum of antenna 1 to a microscopic button, reduction in size and setosity of the mandibular palp and strong dimorphism of the gnathopods imply a more advanced relationship of *Aoroides* to *Lembos* and *Columbaora*.

*Aoroides inermis* n.sp.

Figure 4.

*Type Locality:* Departure Bay, Nanaimo, Vancouver Island, B.C. Bousfield stn. B2, 14 May 1977. Sand, eelgrass, 1-3 m. Holotype ♂, NMC-C-1981-946, paratypes NMC-C-1981-948-950. Mouth of Trevor Channel, Vancouver Island, B.C. Bousfield stn. B18, 30 May 1977. Sand and fine shell, 32-36 m. Allotype ♀ NMC-C-1981-949.

*Material examined:* British Columbia — northern mainland: 2 specimens from Bousfield 1964 stns. H49, H57. Vancouver Island: Approximately 1000 specimens from the collections of Bousfield 1977, 1976, 1975, 1970, 1959, 1955, and the collections of K.E. Conlan, D.V. Ellis, L. Daniels, J.F.L. Hart, G.C. Carl, J.W. Scoggan; southern mainland: 53 specimens from the collections of Bousfield 1978, 1977, 1959 and the collections of C.D. Levings and P. O'Rourke. Washington — approximately 75 specimens from Bousfield 1966 stns. W7, W8, W13, W42.

*Geographic Distribution:* Goose Island, B.C. (51°56'N, 128°26'W) south to Shipwreck Pt., Clallam Co., Washington (48°19'N, 124°27.5'W).

*Ecology:* A boreal species occurring primarily on sand bottoms in the low intertidal and subtidally to 75 m depth on high salinity exposed and protected coasts. Summer temperature: 8.0-18.3°C, salinity 25.6-33+‰. Females ovigerous May-November. This species apparently prefers warmer waters and sandier sediments than other northeastern Pacific species of *Aoroides* and has not been recorded from the Queen Charlotte Islands or Alaska.

*Diagnosis:* Male holotype (5.0 mm). Antenna 2 flagellum weakly setose. Maxilla 1 palp teeth weakly serrated. Maxilliped outer plate teeth smooth below the upper three. Gnathopod 1, coxa 1 slender and elongate, 1 spine and a few setae at the anterodistal corner; segment 2 front and lateral margins densely setose, hind margin bare; segment 3 front margin densely setose; segment 4 tip abruptly narrowed; segment 5 not



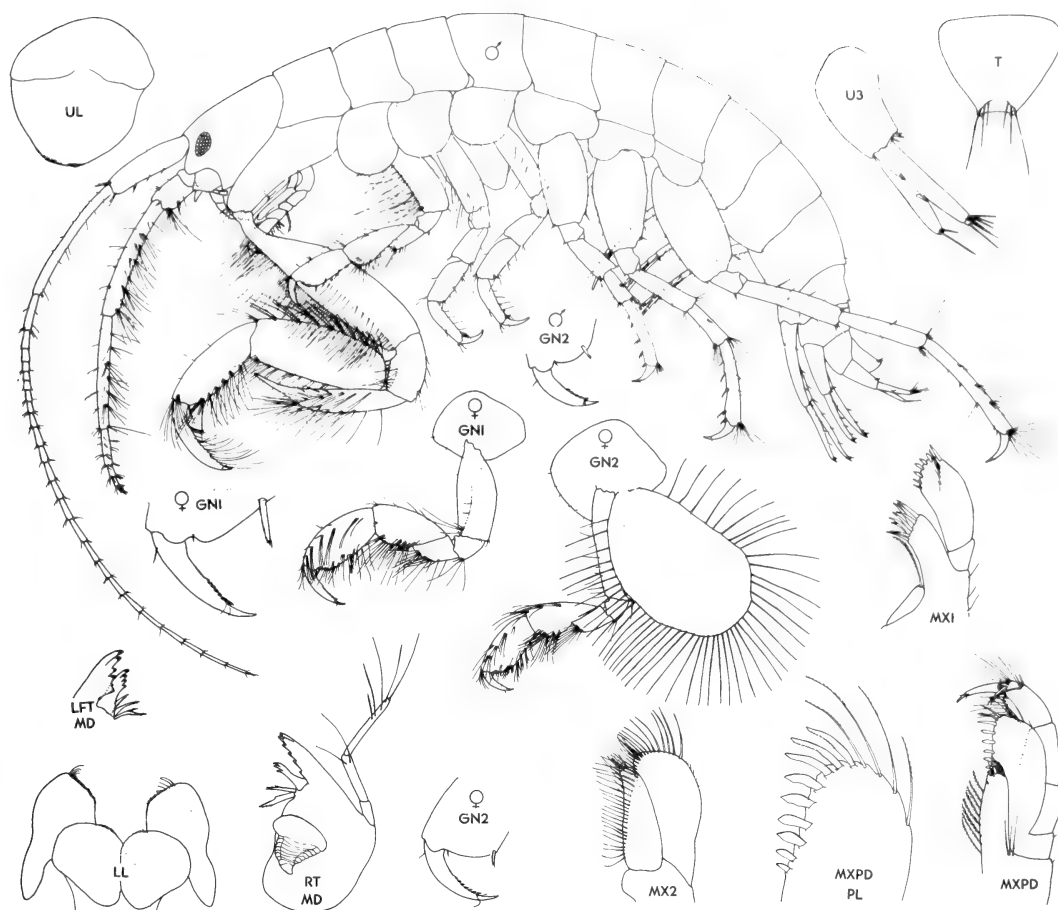


Figure 4. *Aoroides inermis* n.sp. holotype ♂ 5.0 mm, Departure Bay, Nanaimo, Vancouver Is., B.C. 14 May 1977; allotype ♀ 5.5 mm, Trevor Channel mouth, Barkley Sound, Vancouver Is., B.C. 30 May 1977

broader than segment 2, upper margin lined by 8-15 bundles of long setae. Gnathopod 2, palm slightly oblique, dactyl overlapping by more than the length of the nail; coxa with only a few short setae. Peraeopods 3 and 4, segment 5 not spinose. Peraeopod 7, segment 2 slender, marginal setae short. Uropod 3, outer ramus usually lacking lateral spines, but occasionally with 1 or 2 small spines; inner ramus with 0-2 lateral spines.

Pigmentation: Antenna 2 flagellum segment 1 red banded in life. Pigment speckles scattered throughout, concentrating in the lower hind corners of body segments 1-5. Size range: male 3.5-6 mm, female 3-6.5 mm.

Female allotype (5.5 mm). Gnathopod 1, somewhat larger than 2, coxa not enlarged, anterodistal margin of segment 2 bearing a group of long setae, segment 4 not produced, segments

5-7 similar in form to those of gnathopod 2. Otherwise as in the male.

*Etymology*: Refers to the smooth mid and lower inner marginal teeth of the outer plate of the maxilliped.

#### *Aoroides intermedius* n.sp.

Figure 5.

*Type locality*: Haines Island, Barkley Sound, Vancouver Island, B.C. L. Daniels, collector, 8 August 1975. In kelp holdfasts at 3-6 m depth. Holotype ♂, NMC-C-1981-951; Allotype ♀, NMC-C-1981-952; Paratypes NMC-C-1981-953.

*Material examined*: Alaska — southern tip: 87 specimens from Bousfield 1961 stns. A3, A6, A7, A15, A171-2, A174, A175; 50 specimens from Bousfield 1980 stns. S18F3 and S23F1. British Columbia — Queen Charlotte Islands: 52 speci-

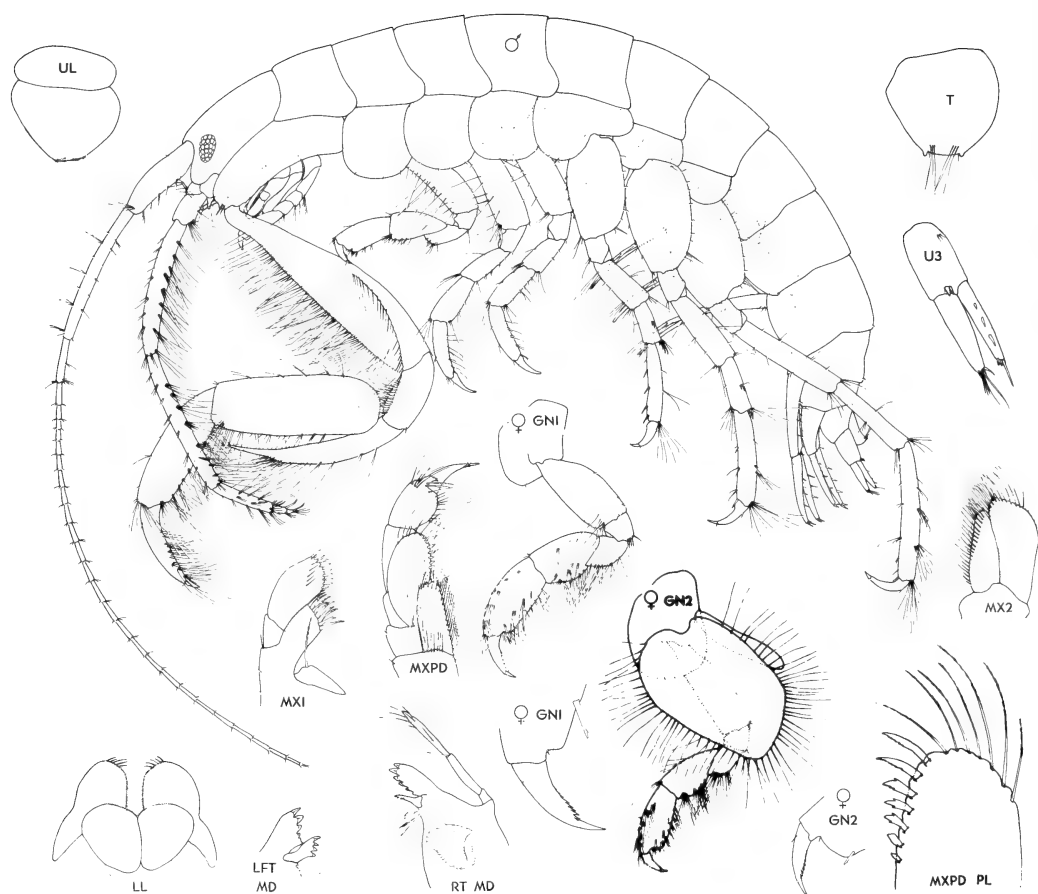


Figure 5. *Aoroides intermedius* n.sp. holotype ♂ 5.0 mm, allotype ♀ 5.5 mm, Haines Is., Barkley Sound, Vancouver Is., B.C. 8 Aug. 1975

mens from Bousfield 1957 stns. E25, H3, H14, W3a, W4a, W8, W12, W14. Northern mainland: approximately 200 specimens from Bousfield 1964 stns. H1, H3, H5, H7, H8, H10, H17, H21, H23, H25, H26, H30, H31, H33, H37, H47, H48, H49, H50, H51, H53, H57, H58, H65. Vancouver Island: approximately 1,000 specimens from the collections of Bousfield 1977, 1976, 1975, 1970, 1964, 1959, 1955, K. Conlan 1976, L. Daniels 1975, D.V. Ellis 1979, J.F.L. Hart and G.C. Carl 1938, and D. Kittle 1972. Southern mainland: 8 specimens from Bousfield 1977 stn. E4, and Bousfield 1955 stn. G4. Washington — approximately 75 specimens from Bousfield 1966 stns. W40, W42.

**Geographic distribution:** Puffin Bay, Baranof Island, Alaska (56°16'N, 134°48'W) south to Mukkaw Bay at Sooes Pt., Clallam Co., Washington (48°19'N, 124°40'W).

**Ecology:** A boreal species occurring amongst algae and eelgrass on sand and gravel bottoms in the low intertidal and subtidally to 63 m on exposed and semi-protected coasts. Summer temperatures from 9.8–15.0°C, salinity 12.8–33+‰. Females ovigerous March to August.

**Diagnosis:** Male holotype (5.0 mm). Antenna 2 flagellum strongly setose. Maxilla 1 palp teeth moderately to strongly serrated. Maxilliped outer plate teeth weakly serrated, lower teeth with 0–2 cusps each. Gnathopod 1 adult coxa slender; segment 2 front and lateral margins densely setose, hind margin bare; segment 3 front margin densely setose; segment 4 tip abruptly narrowed; segment 5 not broader than segment 2, upper margin lined by 5–7 bundles of long setae. Gnathopod 2, palm slightly oblique, dactyl overlapping by more than the length of the nail; coxa with a few short setae only. Peraeopods 3

and 4, segment 5 not spinose. Peraeopod 7, segment 2 broad, marginal setae short. Uropod 3, outer ramus usually lacking lateral spines, but occasionally with 1 or 2 small spines; inner ramus with 0-2 strong lateral spines.

Pigmentation: Antenna 2 flagellum segment 1 red banded in life. Pigment speckles scattered throughout the body, with no concentration in segment corners.

Size range: male 3-5.5 mm, female 3-6 mm.

Female allotype (5.5 mm). Gnathopod 1 somewhat larger than 2, coxa not enlarged, antero-distal margin of segment 2 bearing a group of long setae, segment 4 not produced, segments 5-7 similar in form to those of gnathopod 2. Otherwise as in the male.

*Etymology*: Refers to the serration of the marginal teeth of the maxilliped outer plate, intermediate in degree between *A. inermis* (without) and *A. columbiae* (with).

*Remarks*: The intensity of serration of the maxilliped outer plate teeth is constant with age (although the number of teeth will vary). Table 2 gives the average amount expected. The uppermost 2-3 teeth are always densely serrated as they

blend in size into the marginal plumose setae above. The teeth in the lower two-thirds of the plate are those of diagnostic value.

### *Aoroides columbiae* Walker 1898

Figures 6-8.

*Aoroides columbiae* Walker (1898), p. 285, pl. 16, figs. 7-10; Thorsteinson, 1941, pp. 83-84, pl. 6, figs. 65-66; not Barnard, 1954, pp. 24-26, pl. 22. ? Barnard, 1959, p. 33; ? Barnard, 1961, p. 180; ? Barnard, 1964, pp. 217-218; ? Barnard, 1969, pp. 89-90; ? Barnard, 1970, pp. 68-70, figs. 31-32; ? Nagata, 1960, p. 175, pl. XVI, fig. 94.

*Aoroides californica* Alderman, 1936, pp. 63-66, figs. 33-38.

*Material examined*: Alaska — Amchitka Island: 1 specimen from St. Makarius Bay, P.A. Lebednik, Coll. 1976; southern coast: 83 specimens from Bousfield and McAllister 1961 stns. A6, A7, A48, A75, A81, A87, A91, A96, A147, A151, A153, A165, A168, A171-2, A175; 20 specimens from Bousfield 1980 stns. S4B1-4, S5B2, S11B1, S11B2, S18B1, S21L1, S22F2. British Columbia

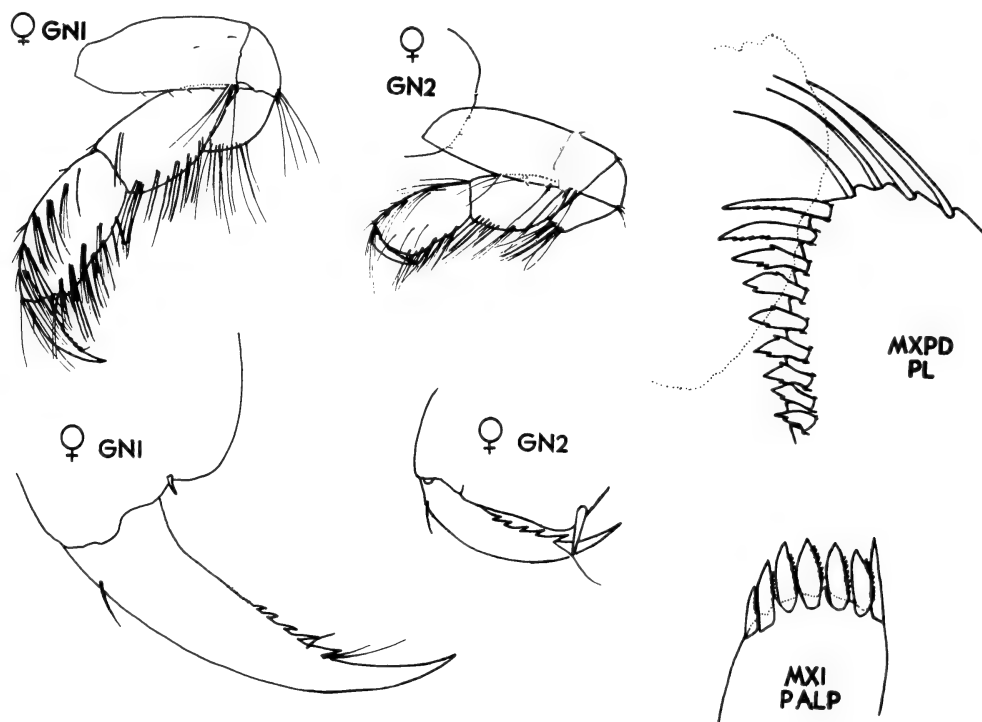


Figure 6. *Aoroides columbiae* Walker, lectotype ♀ 5.0 mm, Puget Sound, Washington, 1897. Illustration of appendages mounted on British Museum slide #1908.3.10.15. The dotted line demarcates an air bubble.

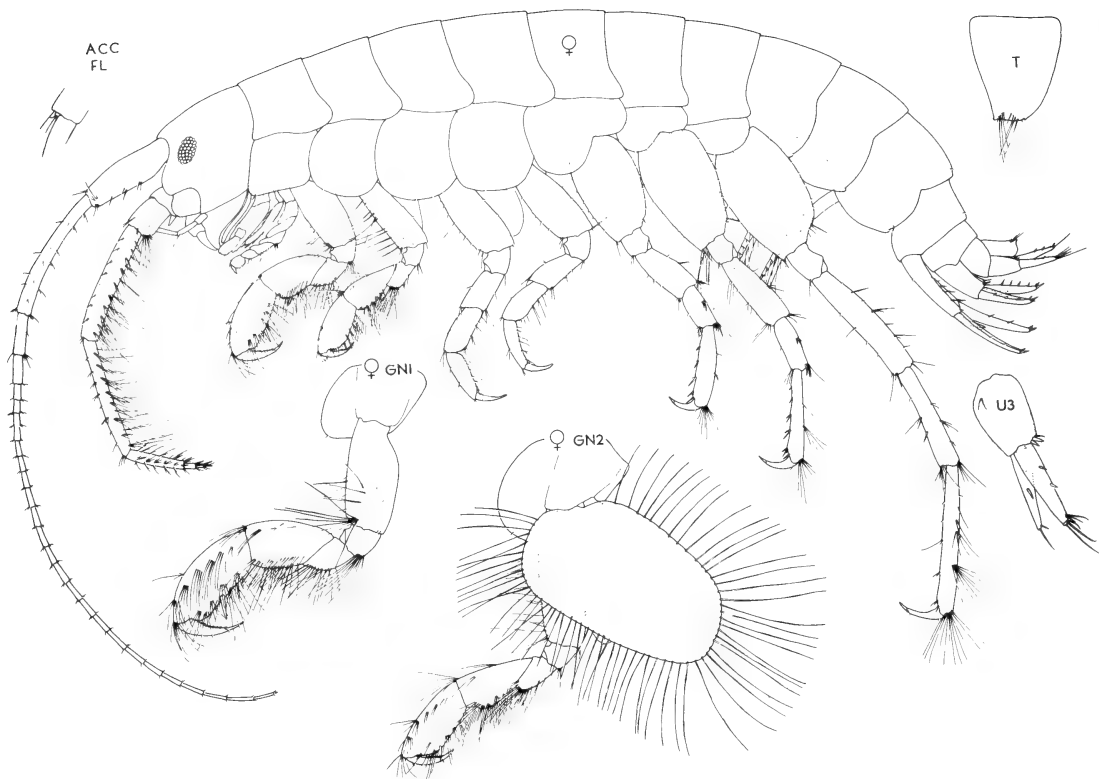


Figure 7. *Aoroides columbiae* Walker, plesiotype ♀ 6.0 mm, Willis Beach, Victoria, Vancouver Is., B.C. 17 May 1977

— Queen Charlotte Islands: 28 specimens from Bousfield 1957 stns. E5, E14a, H2a, H8b, H11, H14, W8, W11, W14, W15b; northern mainland: approximately 250 specimens from Bousfield 1964 stns. H1, H7, H8, H10, H12, H21, H22, H23, H25, H26, H29, H30, H31, H33, H43, H47, H50, H53, H56a, H58, H65; Vancouver Island: approximately 1500 specimens from the collections of Bousfield in 1977, 1976, 1975, 1970, 1959 and 1955 and J.M. Green 1975; southern mainland: 2 specimens from Vancouver Harbour stn. 14, F. Rafi and C. Levings coll. 1976. Washington and Oregon — approximately 80 specimens from Bousfield 1966 stns. W13, W34, W35, W39, W40, W58, W63, W64.

**Geographic distribution:** Amchitka Island, Alaska (51°N, 179°W), south to Oregon (45°26.5'N, 123°57'W); Bahia de San Quintin, Baja California (?); Hawaii (?); Japan (?).

**Ecology:** A boreal species occurring on high salinity exposed and protected coasts amongst algae and sponges or under stones on mixed sand and stony beaches in the low intertidal, to a

depth of 85 m (or to 180 m?). Summer temperatures 8.0–14.5°C, salinity 14.8–33‰. Females ovigerous April–September.

**Diagnosis:** Eyes small, subcircular. Antenna 2 flagellum strongly setose. Maxilla 1 palp teeth weakly serrated. Maxilliped outer plate teeth strongly serrated, lower teeth with 1–4 cusps each. Gnathopod 1 (♂), adult coxa 1 broad, all setae simple; 1 spine and a few setae at the anterodistal corner; segment 2 front and lateral margins densely setose, hind margin bare; segment 3 front margin densely setose; segment 4 tip abruptly narrowed; segment 5 broader than segment 2, upper margin bare except for a small distal bundle of short setae. Gnathopod 1 (♀), anterodistal margin bearing a group of long setae. Gnathopod 2, both sexes, palm slightly oblique, dactyl overlapping by more than the length of the nail; coxa of older males with several long marginal setae. Peraeopods 3 and 4, segment 5 sometimes spinose in the male. Peraeopod 7, segment 2 broad, marginal setae short. Uropod 3, outer ramus usually lacking lateral spines, but occasionally

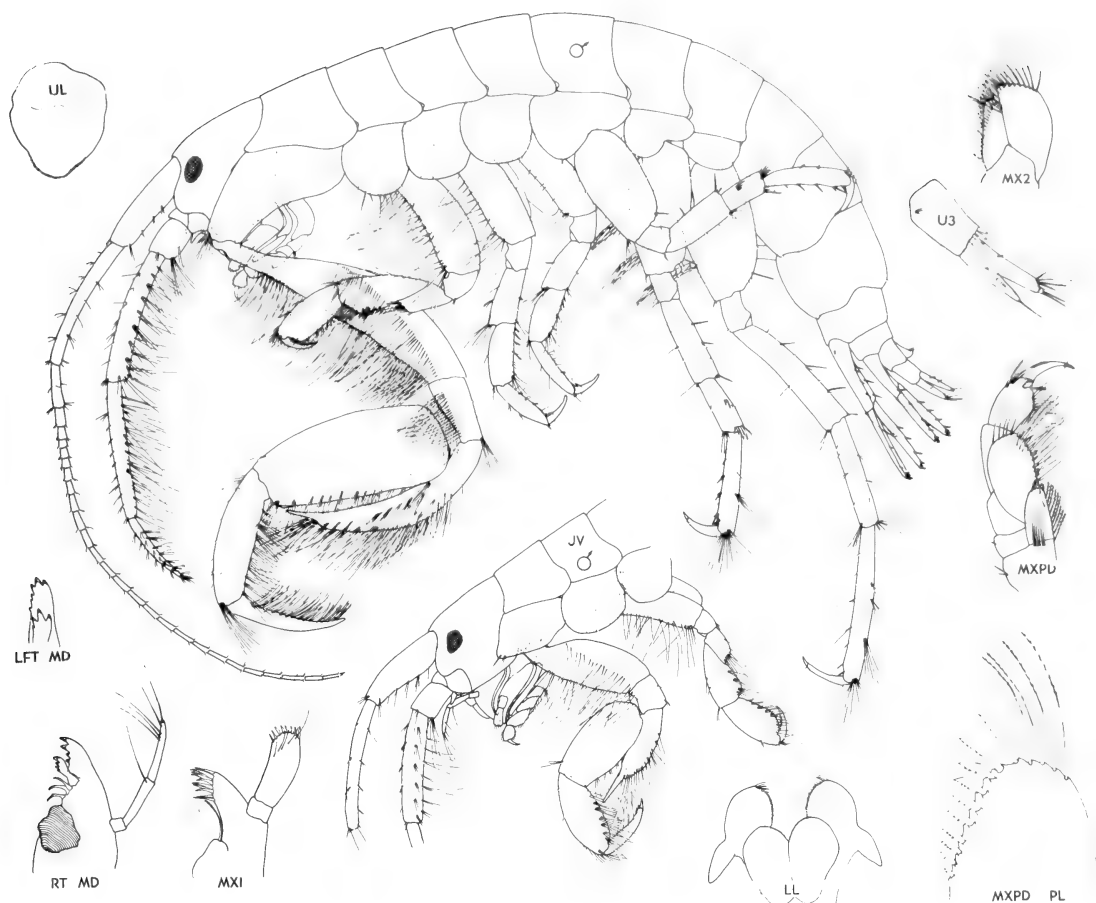


Figure 8. *Aoroides columbiae* Walker plesiotype ♂ 6.0 mm, Willis Beach, Victoria, Vancouver Is., B.C. 18 May 1977. Juvenile plesiotype ♂ 3.5 mm, Witty's Lagoon, Victoria, Vancouver Is., B.C. 17 May 1977

with 1 or 2 small spines; inner ramus with 0-2 strong lateral spines.

Pigmentation: Antenna 2, flagellum not red banded in life. Body segments dark banded; head and parts of segments 6 and 7 white; thereby giving a "saddle-back" pattern.

Size range: male 3.5-6 mm, female 3.5-6.5 mm.

**Remarks:** Only two of Walker's 9 female syntypes remain, these being preserved in slide mounts. British Museum (Natural History) slide #1908.3.10.15 is designated as the holotype because it contains the first gnathopod and maxilliped, the appendages which in combination are diagnostic in the female (see Figs. 5 and 6). The long setae on the anterior margin of gnathopod 1 segment 2 distinguish this species from *A. exilis* n.sp. and *A. spinosus* n.sp., and the serration of the maxilliped outer plate teeth further eliminate *A. inermis* n.sp. *A. intermedius*

closely resembles *A. columbiae* but in *A. intermedius* the lower teeth of the maxilliped outer plate are rarely cusped.

The present male specimens (Fig. 8) resemble Thorsteinson's (1941) male plesiotype in the form of the gnathopods: in gnathopod 1, presence of a distal spine on the coxa, absence of setae on the hind margin of segment 2, segment 5 wider than 2 and lacking dorsal setae; in gnathopod 2, palm oblique, dactyl longer than the palm.

Specimens from Oregon described by Barnard (1954) are almost certainly *A. spinosus* n.sp., as evidenced by the lack of a spine on coxa 1 of the male gnathopod 1, presence of setae on the hind margin of segment 2, reduction of length and number of setae on the anterior margin of segment 2, absence of setae on the anterior margin of segment 3 and gradual, rather than

abrupt, distal narrowing of the older male segment 4.

*Aoroides californica* Alderman (1936), could be synonymous with *A. columbiae* but not for the reasons given by Barnard (1954). The species have in common a lack of lateral spines on the outer ramus of uropod 3, a group of long setae at the anterodistal corner of segment 2 of the female gnathopod 2, absence of dorsal setae on the male gnathopod 1 segment 5 and greater breadth of segment 5 relative to segment 2. However, the body pigmentation (evenly scattered spots) is more indicative of *Aoroides intermedius*. Furthermore, since Alderman failed to illustrate the marginal setae of segment 2, which are present in all male species of the genus, it is conceivable that he could also have overlooked the setae of segment 5 diagnostic of *A. intermedius*.

Re-erection of Alderman's name would therefore necessitate examination of his holotype.

In view of the species diversification within the genus, previous references to *Aoroides columbiae* from southern California and Hawaii by Barnard (1959, 1964, 1969 and 1970) and from Japan by Nagata (1960) require verification, using the diagnostic characters described herein. Similarly, re-examination of *Aoroides nahili* Barnard (1970) of Hawaii is warranted.

***Aoroides exilis* n. sp.**

Figure 9.

*Type locality:* Trial Island Point, Vancouver Island, B.C. Bousfield 1977 stn. B6a, 18 May 1977. *Phyllospadix*, bedrock, *Egredia* and algae, LW-subtidal. Holotype ♂, NMC-C-1981-942; Allotype ♀, NMC-C-1981-943; Paratypes, NMC-

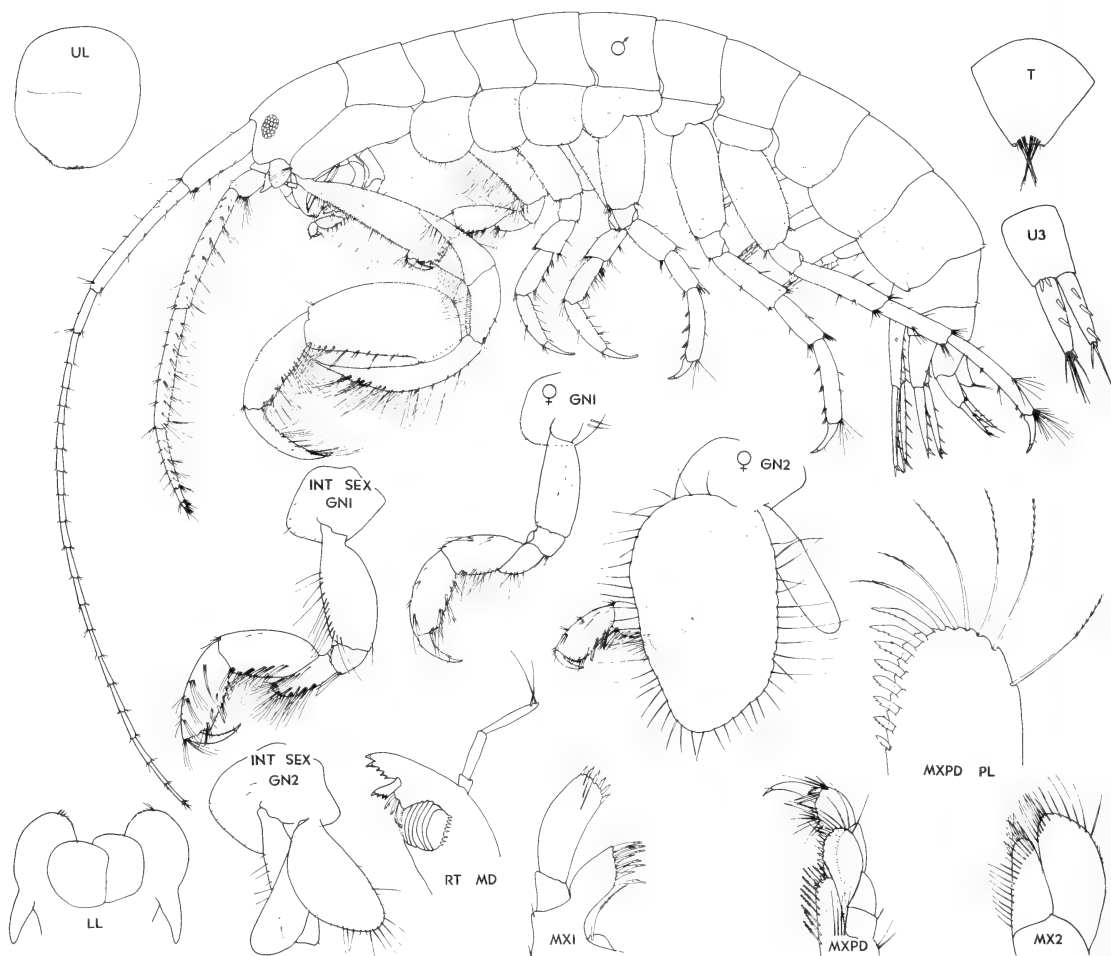


Figure 9. *Aoroides exilis* n.sp. holotype ♂ 4.0 mm, allotype ♀ 5.0 mm, Trial Island Point, Vancouver Is., B.C. 18 May 1977; paratype intersex, Rennison Is., B.C. 20 July 1964

C-1981-944; Rennison Island, B.C. Bousfield 1964 stn. H30, 20 July 1964. Sand and kelp, 7-22 m. Intersex, NMC-C-1981-945. Departure Bay, V.I., Bousfield 1977, stn. B1, May 14, 1977. Paratype immature, NMC-C-1981-947.

*Material examined:* Alaska — southern tip: 79 specimens from Bousfield 1961 stns. A3, A6, A7, A8, A168, A171-2, A174, A175; 30 specimens from Bousfield 1980 stns. S4B1, S20B5, S23F1. British Columbia — Queen Charlotte Islands: 156 specimens from Bousfield 1957 stns. E24, E25, H2, H2a, H3, H5, H8b, H9, W2, W4a, W4b, W8, W11. Northern mainland: approximately 450 specimens from Bousfield 1964 stns. H3, H5, H7, H8, H10, H12, H23, H30, H33, H39, H47, H48, H49, H50, H53, H56a, H57, H65. Vancouver Island: approximately 500 specimens from the collections of Bousfield 1977, 1976, 1975, 1970, 1959, 1955. Southern mainland: 14 specimens from Bousfield 1959 stns. N16, N18, N22. Washington and Oregon — approximately 80 specimens from Bousfield 1966 stns. W8, W18, W30, W34, W36, W40, W64.

*Geographic distribution:* Klokachef Is., Chichagof Is., Alaska (57°25'N, 135°52'W) south to Netart's Bay at Wilson Beach, Tillamook Co., Oregon (45°25.5'N, 123°56'W).

*Ecology:* Occurs amongst algae, eelgrass and sponges under stones and in tide pools on sand and gravel beaches in the low intertidal and subtidally to 50 m depth. Abundant on high salinity exposed coasts, semi- and well protected waters. Summer temperatures 8-15+°C, salinity 12.8-33+‰. Females ovigerous May - August.

*Diagnosis:* Male holotype (4.0 mm). Appendages slender. Antenna 2 flagellum poorly setose. Maxilla 1 palp teeth strongly serrated. Maxilliped outer plate teeth strongly serrated, lower teeth with 2-4 cusps each. Gnathopod 1 coxa slender; segment 2 front and lateral margins densely setose at all ages, hind margin weakly setose; segment 3 front margin densely setose; segment 4 tip abruptly narrowed; segment 5 broader than 2, upper margin bare except for a small distal bundle of short setae. Gnathopod 2, palm transverse, dactyl overlapping only by the length of the nail; coxa of male with several long marginal setae. Peraeopods 3 and 4, segment 5 spinose on hind margin. Peraeopod 7, segment 2 slender, marginal setae short. Uropod 3, both rami with 1-3 strong lateral spines (lateral spines lacking in immatures of less than 3 mm).

Pigmentation: Antenna 2 not red banded in

life. Body segments dark banded; head and parts of segments 6 and 7 white, thereby giving a "saddle-back" pattern.

Size range: male 3.5-5.5 mm, female 2.5-6 mm.

Female allotype (5.0 mm). Gnathopod 1 somewhat larger than 2, coxa not enlarged, antero-distal margin of segment 2 nearly bare, with only a few very short setae, segment 4 not produced, segments 5-7 similar in form to those of gnathopod 2. Otherwise as in the male.

*Remarks:* Figure 8 illustrates the gnathopods of an intersex. The peraeopods and first gnathopod bear small, poorly setose brood plates. The first gnathopod resembles that of an immature male: coxa slightly acute but not elongate, the anterior margin of segment 2 with several long setae and segment 4 somewhat extended below segment 5.

### *Aoroides spinosus* n.sp.

Figure 10.

*Aoroides columbiae:* Barnard, 1954, plate 22 (not Walker, 1898)

*Type locality:* Willis Beach, Victoria, Vancouver Island, B.C. Bousfield 1977 stn. B7a, 19 May 1977. Mud, rock and algae, LW-subtidal. Holotype ♂, NMC-C-1981-954; Allotype ♀, NMC-C-1981-955; Paratypes, NMC-C-1981-956.

*Material examined:* Alaska — southern coast: 110 specimens from Bousfield 1961 stns. A7, A8, A18, A20, A21, A86, A91, A92, A117, A136, A147, A151, A175; 3 specimens from Bousfield 1980 stns. S5B1, S19B1, S19B3. British Columbia — Queen Charlotte Islands: 224 specimens from Bousfield 1957 stns. E5, E14a, E25, H2a, H8b, H9, H11, W1. Northern mainland; 30 specimens from Bousfield 1964 stns. H25, H29, H64. Vancouver Island: 25 specimens from Bousfield 1977 stns. B4a, B6b, B7a, B7b; 10 specimens from Bousfield 1976 stns. B7, B10d, B14; 9 specimens from Bousfield 1975 stns. P17a, P17d; 30 specimens from Bousfield 1970 stns. P709, P715, P717, P718; 31 specimens from Bousfield 1959 stns. O4, O11, V3, V5, V17, V18; 78 specimens from Bousfield 1955 stns. P2, F2, F3, F4, F6, F9, G2, G4; 47 specimens from the collections of K.E. Conlan 1975, J.F.L. Hart and G.C. Carl 1955. Southern mainland: 61 specimens from Bousfield 1959 stns. N11, N17, N18. Washington and Oregon — 11 specimens from Bousfield 1966 stns. W7, W64.

*Geographic distribution:* Prince William Sound, Alaska (60°44'N, 146°10'W) south to Netart's Bay

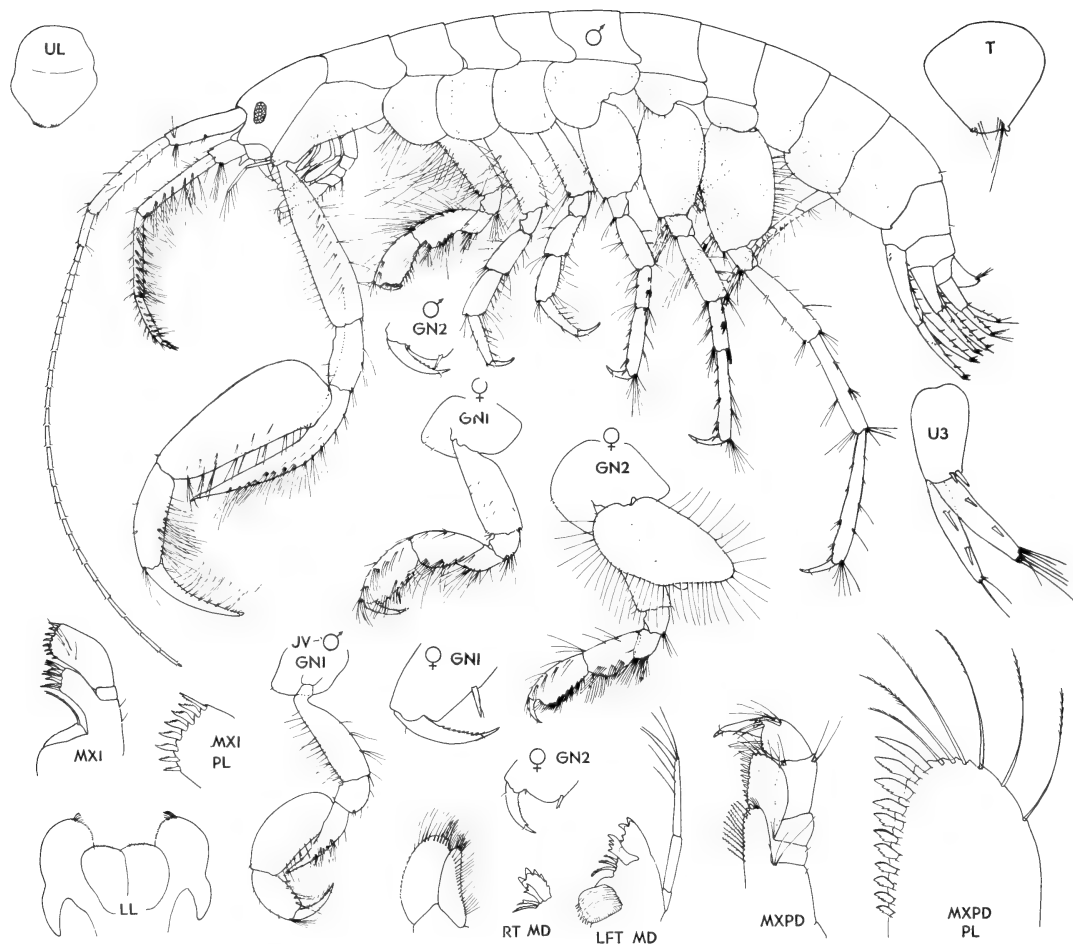


Figure 10. *Aoroides spinosus* n.sp. holotype ♂ 5.5 mm, allotype ♀ 6.0 mm, Willis Beach, Victoria, Vancouver Island, B.C. 19 May 1977

at Wilson Beach, Tillamook Co. Oregon (45°25.5'N, 123°56'W). Coos Bay (Barnard, 1954)?

**Ecology:** Occurs amongst algae and debris on mixed sand, gravel sediments and bedrock in the low intertidal and subtidally to 45 m depth. Abundant in meso- to polyhaline, semi- and well-protected waters. Summer temperatures 8-16°C, salinity 12.8-32‰. Females ovigerous April-August.

**Diagnosis:** Male holotype (5.5 mm). Appendages slender. Antenna 2 flagellum poorly setose. Mandibular palp segment 2 lacking setae, segment 3 with 2-6 setae. Maxilla 1 palp teeth strongly serrated. Maxilliped outer plate teeth strongly serrated, lower teeth with 2-3 cusps each. Gnathopod 1 coxa slender; segment 2 front and lateral margins poorly setose, setae reducing in number and length with age, hind margin

weakly setose; segment 3 front margin nearly bare; segment 4 tip gradually narrowed; segment 5 broader than 2, upper margin bare except for a small distal bundle of short setae. Gnathopod 2, palm transverse, dactyl overlapping only by the length of the nail; coxa of male with several long marginal setae. Peraeopods 3 and 4, segment 5 not spinose. Peraeopod 7, segment 2 broad, marginal setae long in male. Uropod 3, both rami with 1-3 strong lateral spines (lateral spines lacking in immatures of less than 3 mm).

**Pigmentation:** Antenna 2 not red banded in life. Body segments light brown, pigment diffusely speckled.

**Size range:** male 3.5-7 mm, female 3.5-6.5 mm.

Female allotype (6.0 mm). Gnathopod 1 somewhat larger than 2, coxa not enlarged, anterodistal margin of segment 2 nearly bare, with only a few very short setae, segment 4 not produced,



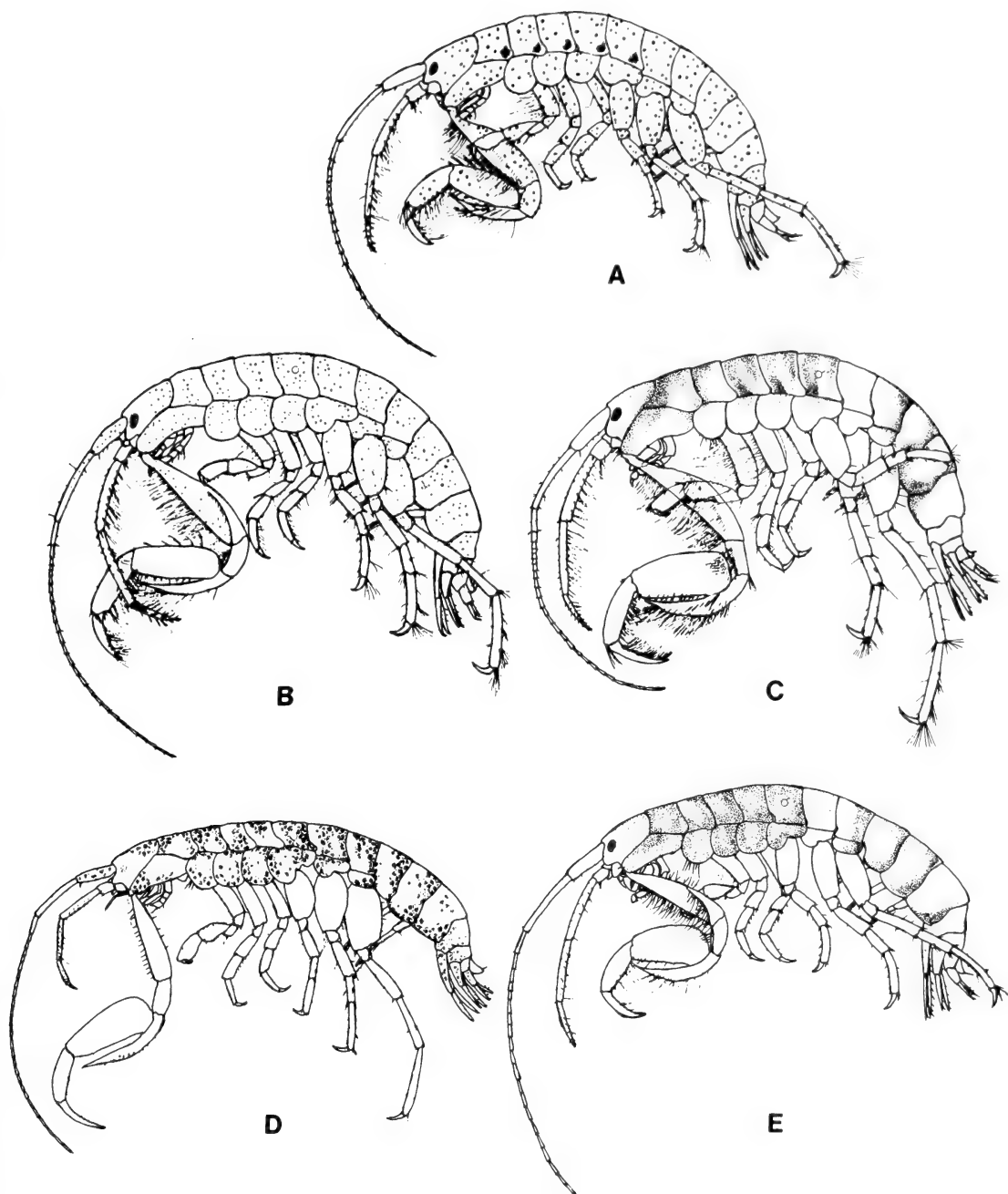


Figure 11. Body pigmentation patterns in *Aoroides*.

A. *A. inermis*. B. *A. intermedius*. C. *A. columbiae*. D. *A. exilis*. E. *A. spinosus*.

segments 5-7 similar in form to those of gnathopod 2. Otherwise as in the male.

*Remarks:* *A. spinosus* also shows a tendency to intersex. Six intersexes were noted in material from Vancouver Island near Victoria and another from the Queen Charlotte Islands.

Juvenile males are distinguishable from other juveniles by the slender second gnathopod, the setose hind margin of segment 2 of the first gnathopod and paucity of setae on the front margin (Fig. 10.)

Barnard's (1954) *Aoroides columbiae* is clearly not this species but *Aoroides spinosus*. The shape of the first gnathopod is distinctive in the setation pattern of coxa and segments 2, 3 and 5, the shape of segment 4 and the larger size of segment 5 relative to segment 2. His comments about growth variability in *Aoroides columbiae* must be viewed with the consideration that more than one species was being examined.

## Discussion and Conclusions

### *Biogeography and Ecology*

Tables 3 and 4 summarize the geographic and ecological distributions of the northeastern Pacific Aoridae. All species occur amongst algae and debris on mixed sediments in the intertidal and subtidally to the limits of the photic zone. The species are restricted to meso- and polyhaline waters, generally on open and semi-protected coasts. The genus *Aoroides* ranges through the entire boreal coast. *A. inermis* is the most restricted of the species, failing to penetrate into Alaska and occurring primarily on sandy substrates. *Columbaora* and *Lembos* (*Lembos*) occur in more southerly waters. The present record for *Lembos concavus* is its most northerly extension in the northeastern Pacific coastal region. *Lembos* (*Arctolembos*) is a rare arctic genus, this present record extending its range eastward to the Bering Sea.

### *Taxonomic considerations*

Within the superfamily *Corophioidea*, the *Aoridae* appear to be most closely related to the *Isaeidae* (*Photidae*), and the new family *Neomegamphopidae* (Myers, 1981) which also show strong development of the first gnathopod. *Lembos* (*Arctolembos*), the most primitive of the northeastern Pacific Aoridae, possesses many characteristics in common with the primitive photid *Protomedeia*. Subsequently, in increasing

order of advancement, are *Lembos* (*Lembos*), *Columbaora* and *Aoroides*. These genera trend phylogenetically towards reduction of the accessory flagellum, weakening of the mandibular palp, reduced setation of the maxilla 1 inner plate, increasing dimorphism of the gnathopods, loss of the hind setae on segment 2 of the appendages and loss of the marginal setae on epimeron 2.

Comparison of the merochelate genus *Aora*, which occurs in the Indo-Pacific and Atlantic, indicates a close resemblance with *Lembos* (*Lembos*) and *Columbaora* in the form of the female gnathopods, semi-falcate to falcate mandibular palp and prominent accessory flagellum.

Phyletic relationships therefore seem to link these Aoridae in the order, *Protomedeia* to *Lembos* to *Columbaora* to *Aora*, with *Aoroides* being an outlier, possibly a derivative of *Columbaora*, rather than of *Aora*. This linkage may be bidirectional, as Barnard (1973) indicates, with the *Columbaora-Aora-Aoroides* line originating separately from *Lembos*. The latter would subsequently have led to *Lembopsis* and *Lemboides*.

Within the genus *Aoroides*, close similarity of the component species suggests a relatively recent evolution. The northeastern Pacific species are divisible into two groups: the stouter bodied, more setose group comprising *A. columbiae*, *A. intermedius* and *A. inermis*, and a more slender bodied, less setose group comprising *A. exilis* and *A. spinosus*. The individual species relate to each other in the presented order: *A. columbiae* with strongly cusped maxilliped teeth and dorsally bare segment 5, leading through *A. intermedius* as its name implies, to *A. inermis* with smooth maxilliped outer plate teeth and dorsally setose 5th segment of the male gnathopod 1. The second group has in common with *A. columbiae* the cusped maxilliped teeth, the dorsally bare segment 5, enlarged segment 5 in relation to segment 2, setose male coxa 2, and stronger body pigmentation. *A. exilis* appears to be more closely related to *A. columbiae* than does *A. spinosus* by having in common a similar pigmentation pattern and strong setation on the male gnathopod 1 segments 2 and 3. The first gnathopod of the male *A. spinosus*, which shows stronger setation and similar form in the juvenile, with age becomes poorly setose and greatly elongated to hang way below the body.

The two groups appear to be sufficiently dissimilar to suggest that the gradient of evolu-

tion was not linearly from *A. inermis* to *A. spinosus*, but bidirectional; thus, from a hypothetical ancestral type evolved in one direction *A. columbiae* and thence *A. intermedius* and *A. inermis*, and in the other direction *A. exilis* and *A. spinosus*. The ecological data of Tables 3 and 6 give some support to this hypothesis. *A. columbiae* is the most primitive and most widely distributed of the five species, having spread north into the Alaskan Aleutian Islands, possibly westward into Japan, and possibly also southward into Hawaii and Baja California (assuming that species identifications outside of this study area are accurate). *A. intermedius* and *A. exilis* have a narrower but similar distribution with a focal point in British Columbia, while *A. spinosus* spans a more northerly range and *A. inermis* is restricted to warmer waters and a narrower habitat. The two species of *Aoroides* not found in the northeastern Pacific, *A. secundus* Gurjanova\* and *A. nahili* Barnard, were probably derived from the Asian Pacific and Hawaiiin populations of *A. columbiae* respectively.

## Acknowledgements

We wish to thank the many donors of valuable material, too numerous to list, and the British Museum of Natural History for the loan of A.O. Walker's type specimens of *Aoroides columbiae*. We are greatly indebted to Mrs. F. Zittin of Vancouver, B.C. for her capable execution of the illustrations.

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\*Preliminary examination of material of *Aoroides secundus* Gurjanova 1938 from the Okhotsk Sea, kindly supplied very recently by Dr. Nina Tzvetkova, Zoological Museum, Leningrad, indicates that this species is intermediate between the *A. exilis-spinosus* group, and the *A. columbiae-inermis-intermedius* group, with somewhat closer affinities (overall) to the former group.

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<sup>1</sup>References not cited herein are listed in Barnard (1969)

**Table 1. Uncommon characteristics of *Lembos (Arctolembos) arcticus***

Character	Differences from <i>Lembos (Lembos)</i>
Head lobe	shallower
Eye	smaller
Lower lip	mandibular lobes not acutely attenuated
Maxilla 1 inner plate	lacking a long apical seta, bearing many fine setae <sup>1</sup>
outer plate	bearing more than 10 spines
Maxilliped outer plate	shorter
palp segment 2	more elongate
Coxae	deeper, especially the anterior lobe of coxa 5
Gills	smaller, plate-like
Gnathopod 1 segment 6	subchelate, relatively small and unaltered <sup>2</sup>
Gnathopods 1 and 2, Peraeopods	posterior margin bearing a group of long setae
3 and 4, segment 2	
Peraeopods 5-7, segment 2	hind margin densely setose <sup>1</sup>
dactyls	lengthen posteriorly
Uropods 1 and 2, rami	sinuous <sup>1</sup>
Uropod 3, outer ramus	setose as well as spinose <sup>2</sup>

<sup>1</sup>Similar to *Protomedeia*<sup>2</sup>Similar to *Leptocheirus***Table 2. Range in number of cusps on the maxilliped outer plate teeth of *Aoroides inermis*, *A. intermedius* and *A. columbiae*.**

Tooth No. uppermost to lowermost	Range in number of cusps per tooth*		
	<i>A. inermis</i> (18 obs.)	<i>A. intermedius</i> (10 obs.)	<i>A. columbiae</i> (12 obs.)
1	0-15	4-9	5-15
2	0-15	4-8	2-13
3	0-4	1-4	3-8
4	0	0-3	2-9
5	0	0-1	1-7
6	0	0-1	2-6
7	0	0-1	2-8
8	0	0-1	0-4
9	0	0-1	1-4
10	0	0	1-3
11	0	0	1-3

\*Values are given for 3.5-7 mm individuals. Specimens with fewer teeth carry the same range in values.

**Table 3. Distribution of Boreal Northeastern Pacific Aoridae Listed in Geographic Order**

Species	Aleutian Is., Alaska	Prince William Sd., Alaska	Cross Sd. To Dixon Ent., Alaska	Northern B.C. and Queen Charlotte Is., B.C.	Central B.C. and Vancouver Is., B.C.	Washing- ton	Oregon	Other Records
<i>Lembos (Arctolembos) arcticus</i>	X	Θ	Θ	Θ	Θ	Θ	Θ	Kara Sea
<i>Aoroides columbiae</i>	x	X	X	X	X	X	X	Baja California ? Hawaii? Japan ?
<i>Aoroides spinosus</i>	Θ	X	X	X	X	x	x	
<i>Columbaora cyclocoxa</i>	Θ	Θ	x	X	X	x	Θ	
<i>Aoroides intermedius</i>	Θ	Θ	x	X	X	X	Θ	
<i>Aoroides exilis</i>	Θ	Θ	x	X	X	X	X	
<i>Aoroides inermis</i>	Θ	Θ	Θ	X	X	X	Θ	
<i>Lembos concavus</i>	Θ	Θ	Θ	Θ	X	Θ	Θ	Southern California
Number of species	2	2	5	6	7	6	3	

X Abundant; x Occasional; Θ Absent

**Table 4. Habitats of Boreal Northeastern Pacific Aoridae**

Species	Coastal Exposure		Salinity Range				Depth Range			Substrate
	Open and semi- protected	Protected and Estuarine	Marine Polyhaline ( $> 28^{\circ}/_{\infty}$ )	Mesohaline ( $10-27^{\circ}/_{\infty}$ )	Oligo- haline ( $1-9^{\circ}/_{\infty}$ )	Fresh- water ( $< 1^{\circ}/_{\infty}$ )	$> 25$ m	1-25 m	LW-MW	
<i>Lembos (Arctolembos) arcticus</i>	X	Θ	X	Θ	Θ	Θ	X	Θ	Θ	Sandy sediment
<i>columbiae</i>	X	X	X	X	Θ	Θ	x	X	X	Amongst algae, eelgrass and wood debris on mixed sediments
<i>Aoroides spinosus</i>	X	X	X	X	Θ	Θ	x	X	X	Amongst algae, eelgrass, wood debris on mixed sediments
<i>Columbaora cyclocoxa</i>	X	Θ	X	Θ	Θ	Θ	Θ	X	X	Amongst algae and eelgrass on coarse sediments
<i>Aoroides intermedius</i>	X	Θ	X	X	Θ	Θ	X	X	X	Amongst algae, eelgrass, sponges and tunicates on coarse sediments
<i>Aoroides exilis</i>	X	X	X	x	Θ	Θ	Θ	X	X	Amongst algae, eelgrass, wood debris, sponges and tunicates on mixed sediments
<i>Aoroides inermis</i>	X	X	X	x	Θ	Θ	X	X	X	Amongst algae on sandy sediment
<i>Lembos concavus</i>	X	Θ	X	Θ	Θ	Θ	Θ	X	Θ	Amongst algae on stony substrate

X Abundant; x Occasional; Θ Absent

**Table 5. Specimens of Aoridae Designated for Deposition in the Smithsonian Institution (USNM) and Zoological Museum (Leningrad, USSR).**

Species	Smithsonian Institution (USNM)			Zoological Museum (Leningrad USSR)		
	National Museums Accession No.	Station No.	No. Specimens	National Museums Accession No.	Station No.	No. Specimens
<i>Aoroides inermis</i> *	1977-181	B2	2 ♂♂, 2 ♀♀	1977-181	B2	2 ♂♂, 2 ♀♀
<i>Aoroides intermedius</i> *	1975-205	Haines Is.	2 ♂♂, 2 ♀♀	1975-205	Haines Is.	2 ♂♂, 2 ♀♀
<i>Aoroides columbiae</i> *	1976-157	B7	2 ♂♂, 2 ♀♀	1976-157	B7	2 ♂♂, 2 ♀♀
<i>Aoroides exilis</i> *	1977-181	B6b.	2 ♂♂, 2 ♀♀	1977-181	B1	2 ♂♂, 2 ♀♀
<i>Aoroides spinosus</i> *	1959-112	V17	2 ♂♂, 2 ♀♀	1959-112	V3	1 ♂
<i>Aoroides spinosus</i>				1977-181	B7a	2 ♀♀
<i>Columbaora cyclocoxa</i> *	1970-152	P710	1 ♂, 1 ♀, 1 jv.	1964-198	H5	1 ♂, 1 ♀, 2 jv.

\*Material also deposited in the British Museum (Natural History) London.





# Studies on the amphipod family Lysianassidae in the Northeastern Pacific region. *Hippomedon*: and related genera Systematics and distributional ecology

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## ABSTRACT

This study analyzes the systematics and distributional ecology of the genus *Hippomedon* (sens. lat.), a group of medium large, mainly infaunal lysianassid amphipod crustaceans, in shallow waters of the northeastern Pacific coastal marine region. Utilizing numerical taxonomic methodology, the 17 regional species are grouped in four genera, viz. *Hippomedon* (sens. str.), the most apomorphic group, containing about 40 species world-wide of which 10 occur in the North Pacific and of which *H. columbianus* n.sp. is newly described; the monotypic, intermediate *Paratryphosites* Boeck of Arctic and North Atlantic regions; the relatively primitive *Wecomedon* new genus, consisting of five species endemic to the North Pacific region and of which *W. similis* is newly described, and the most primitive genus *Psammonyx* Bousfield, consisting of four species, two of which are endemic to the northwestern Atlantic region, and two, *P. kurilicus* (Gurjanova) and *P. longimerus* new species are endemic to the North Pacific. Keys, figures and diagnoses are provided for the regional species and genera.

## RÉSUMÉ

Il s'agit d'une étude taxinomique et de distribution écologique du genre *Hippomedon* (*sensu lato*), un groupe de crustacés amphipodes lysianassidés de taille moyenne et se rencontrant surtout sur les hauts-fonds des eaux côtières dans le nord-est du Pacifique. Suivant une méthodologie propre à la taxinomie numérique, l'auteur groupe les dix-sept espèces de la région en quatre genres : 1<sup>e</sup> *Hippomedon* (*sensu stricto*), le groupe le plus évolué (quarante espèces dans le monde, dont dix dans le Pacifique nord), dont *H. columbianus* n.sp. décrit ici pour la première fois ; 2<sup>e</sup> *Paratryphosites* Boeck de l'Arctique et de l'Atlantique nord, genre monotypique et intermédiaire ; 3<sup>e</sup> *Wecomedon*, genre relativement primitif nouvellement décrit, constitué de cinq espèces indigènes dans le Pacifique nord, y compris *W. similis* décrit ici pour la première fois ; 4<sup>e</sup> *Psammonyx* Bousfield, genre le plus primitif, constitué de quatre espèces dont deux sont indigènes au nord-ouest de l'Atlantique et deux, de nouvelles espèces *P. kurilicus* (Gurjanova) et *P. longimerus*, sont indigènes au Pacifique nord. Des illustrations, des données techniques d'identification et des clés des genres et des espèces de la région étudiée apparaissent dans ce travail.

## Introduction

The lysianassid genus *Hippomedon* (sens. lat) comprises about 75 species of benthic fossorial amphipod crustaceans that occur mainly in sub-arctic and boreal coastal marine regions of the northern hemisphere. Several species are known from littoral and sublittoral regions of the southern hemisphere and a few have been recorded offshore and from the abyss. In the North Pacific region (Pacific rim) a total of 13 species and 4 subspecies have previously been recorded. Gurjanova (1962) included 6 species and 2 subspecies from the northwestern Pacific,

including the Sea of Okhotsk and Japan Sea. Holmes (1908), Shoemaker (1955), Barnard (1954, 1964b, 1966, 1971), and Hurley (1963) have collectively treated an additional 6 species and 3 subspecies or forms from the northeastern (North American) Pacific coast, from Point Barrow, Alaska to California. However, much of the Pacific rim coastal marine region remains virtually unsampled with respect to material of *Hippomedon*. Furthermore, the present basis for recognition of the genus and species composition encompasses major taxonomic problems. The

present study was undertaken in an attempt to fill this distributional hiatus and to resolve these taxonomic problems.

This study utilizes extensive lysianassid material from the northeastern Pacific region obtained by field expeditions of the National Museum of Natural Sciences since 1955 (see Bousfield (1958, 1963, 1968), Bousfield and McAllister (1962) and Bousfield and Jarrett (in press) for pertinent station lists). Other source material in the NMNS and in other museums have been utilized, as noted in the text. Recently material from Vancouver Island and southeastern Alaska has been collected and photographed live by E.L. Bousfield and Mr. Ron Long, Simon Fraser University, and the resulting slide transparencies have been utilized in some of the species descriptions.

## SYSTEMATIC SECTION

**Family Lysianassidae** Dana, 1849 (emend. Bousfield, 1979)

**Subfamily Uristidinae** Hurley, 1963

In an attempt to subdivide the large and unwieldy family Lysianassidae into natural groupings of allied genera, Hurley (1963) tentatively proposed the subfamilies Uristidinae and Lysianassinae. Although these two subfamilies as defined would encompass less than half the known lysianassid genera, Hurley (1963) did include the genus *Hippomedon* (and allied genera) in the subfamily Uristidinae. This subfamily is characterized primarily by a subchelate or imperfectly subchelate first gnathopod. Additional features include: antenna 1, peduncle generally not carinate; antenna 2, peduncular segments not noticeably dilated; coxal plates 1 and 2 not appreciably smaller than 3 and 4; coxal plate 1, lower front angle not hidden by

coxal plate 2; uropod 3 biramous. This subfamily delineation is very incomplete and does not clearly demonstrate a natural or phyletic basis for its recognition. However, component genera appear somewhat more plesiomorphic than that of Lysianassinae in the following morphological tendencies: mouthparts basic (e.g., mandibular molar present and palp inserted opposite or distal to molar); coxal gills simple; uropod 3 usually natatory; telson lobes usually separate. The subfamily Uristidinae also includes the genera *Uristes*, *Tryphosa*, *Orchomenella*, *Anonyx* and *Allogaussia*.

The genus *Hippomedon* was first established by Boeck (1870) with the Arctic species *Anonyx holbolli* Krøyer, 1846, as the type, and for many years encompassed species mainly from the North Atlantic and Arctic oceans. The genus was distinguished from other lysianassid genera by such characters as a short first antenna with a large first flagellar segment and comparatively small accessory flagellum, a slender first gnathopod with an oblique palm and a long dactyl, a tooth on the third epimeral plate, a gill on peraeopod 7, rami of uropod 3 not setose, and an oblong, deeply cleft telson.

Gurjanova (1962) fused *Paratryphosites* to *Hippomedon* and Barnard (1969) provisionally synonymized with it also *Paracentromedon* Chevreux and Fage, 1925, and *Elimedon* J.L. Barnard, 1962. The fusion of genera and the subsequent submerging and assignation of many new species within *Hippomedon* has resulted in a morphologically diverse genus which is excessively large, poorly defined, and taxonomically unwieldy. In this study, endemic North Pacific species, type North Atlantic and other selected species have been re-examined on the basis of 23 taxonomic characters of presumed or probable generic value. (see Tables 1 & 2). The above species are grouped into distinct genera as diagnosed in the text and in the key below.

### Key to *Hippomedon* and Related Genera

1. Mandible, palp segment 3 very short, length  $\frac{1}{2}$  or less segment 2 ..... 2  
Mandible, palp segment 3 normal, length nearly equal to segment 2 ..... 3
2. Telson lobes fused  $\frac{1}{2}$  or greater ..... *Elinedon*  
Telson lobes fused  $\frac{1}{4}$  ..... *Paracentromedon*
3. Telson short, lobes fused  $\frac{1}{2}$  or more, each lobe broad, with 7 to 9 pical spines; antenna 2 more than twice as long as antenna 1; gill peraeopod 7 lacking .....  
..... *Paratryphosites* Stebbing, restored status (p. 120)

- Telson long, lobes fused basally less than  $\frac{1}{2}$  length, each lobe broad, with 1-5 apical spines; if antenna 2 more than twice as long as antenna 1, gill peraeopod 7 present ..... 4
4. Antenna 1, basal flagellar segments fused (conjoint per Barnard 1967); telson lobes well tapered, apices with single spine (rarely 2-3); coxal gill on peraeopod 7 present, small ..... *Hippomedon* Boeck, *sens. str.* (p. 105)
- Antenna 1, basal flagellar segments not conjoint; telson lobes weakly or not tapered, apices truncate, with multiple spines; coxal gill on peraeopod 7 lacking ..... 5
5. Antenna 1, peduncular segments 2 and 3 each longer than flagellar segment 1, not telescoped, peraeopod 5 much (25%) shorter than peraeopods 6 and 7; peraeopod 7 longest ..... *Psammonyx* Bousfield emend. (p. 118)
- Antenna 1, peduncular segments 2 and 3 each shorter than flagellar segment 1; peraeopod 5 slightly shorter than peraeopod 6, peraeopod 6 longest ..... *Wecomedon* new genus (p. 113)

**Genus *Hippomedon*** Boeck, 1870 (*sens. str.*, revised)

*Hippomedon*

- Sars, G.O., 1895, p. 55
- Stebbing, T.R.R., 1906, p. 58
- Gurjanova, E.F. 1962, p. 93 (part, excluding *Paratryphosites*)
- Hurley, D.E., 1963, p. 135 (part)
- Barnard, J.L., 1964a, p. 5 (part)
- Barnard, J.L., 1969, p. 345 (part, excluding *Paracentromedon*, *Elimedon* and *Paratryphosites*)
- Bellan-Santini, D. 1965, p. 161 (part)

**Diagnosis:** Body slender, elongate. Head small, partially hidden by coxa 1. Eyes imperfectly developed, often not visible in preserved specimens. Coxal plates 1-4 moderately deep, narrow. Epimeral sideplate 3 produced posterodistally into an upturned tooth. Antenna 1 short, peduncular segment 1 inflated, more or less produced anterodistally into a beak-shaped process; segments 2 and 3 short, deep, telescoping into 1; flagellum, proximal segments fused (conjoint); accessory flagellum relatively short. Antenna 2 slender, much longer than antenna 1; flagellum of antenna 1 and antenna 2 calceolate in male only. Mandibular molar strong, ridged; palp slender, level with or slightly distal to molar; segment 2 with a distal setal row; segment 3 more than  $\frac{1}{2}$  the length of segment 2, medial margin with comb setae. Maxilla 1, palp with broad segment 2, bearing a row of apical spine-teeth; outer plate with eleven apical pectinate spine-teeth; inner plate with 2-5 apical plumose setae. Maxilla 2, inner plate slightly shorter and broader than outer. Maxilliped, outer plate reaches well beyond segment 2 of palp, inner plate bearing three strong teeth and two spines apically, a row of plumose setae medially. Gnathopod 1, segment 6, palm long, oblique, usually weakly

defined; dactyl long, slender. Peraeopods 3 and 4, dactyls long, slender. Peraeopod 5 not shortened, segment 2, hind margin tapering distally. Peraeopods 5, 6 and 7, distal segments slender; peraeopod 6 slightly longer than 5 and 7. Coxal gills simple on peraeopods 2, 3 and 4, lobed on 5 and 6, simple, reduced on 7. Uropod 3, rami spinose, not setose. Telson oblong, lobes fused basally, each tapering distally, apex with single apical spine (rarely 2).

**Type species:** *Hippomedon holbolli* (Krøyer, 1846)

**Remarks:** To date, 42 species of *Hippomedon* (*sens. str.*) are known in the world; most are recorded from the North Atlantic and Arctic oceans, but 6 species are known from the southern hemisphere, especially the Tasman Sea. *H. geelongi* Stebbing, 1888, from Australia, *H. tracatrix* Barnard, 1971, from Oregon, *H. macrocephalus* Bellan-Santini, 1972, from Antarctica, and *H. incisus* K.H. Barnard, 1930, from New Zealand, are questionably included in this genus. Although their original limited descriptions (in the literature) do not conform with the present generic diagnosis, these three species are retained in *Hippomedon* (*sens. str.*) until specimens can be examined and all characters analyzed.

Barnard (1964) provisionally synonymized *Paracentromedon* Chevreux and Fage, and *Elimedon* Barnard with *Hippomedon*. However, the unexpanded coxa 1, the short second antenna, the short third segment of the mandibular palp and the narrow segment 2 of peraeopod 5 and 6 exclude both of these genera from *Hippomedon* (*sens. str.*) Barnard (1969) includes *Paratryphosites* in his different brief diagnosis of *Hippomedon*, so that his diagnosis of the telson differs from that given above for *Hippomedon* (*sens. str.*).

# Key to North Pacific and Related Species of *Hippomedon* (*sens. str.*)

1. Epimeral sideplate 3 with basal notch dorsal to the posterodistal tooth (rudimentary on coecus) ..... 2  
Epimeral sideplate 2 without notch dorsal to the posterodistal tooth ..... 5
2. Gnathopod 2, palm long, concave, dactyl much shorter than palm ..... *columbianus* n.sp. (p. 109)  
Gnathopod 2, palm short, dactyl equal to palm ..... 3
3. Antenna 1, peduncular segment 1 strongly produced anterodistally into an acute process, reaching beyond segment 2 (North Atlantic) ..... *denticulatus* (Bate) (p. 108)  
Antenna 2 peduncular segment 1 not strongly produced anterodistally, not reaching beyond segment 2 (North Pacific) ..... 4
4. Uropod 3, rami broad, margins parallel, tapering only at the tips, segment 2 of outer ramus short ..... *orientalis* Gurjanova (p. 112)  
Uropod 3, rami with margins gradually tapering distally, segment 2 of outer ramus relatively elongate ..... *coecus* (Holmes)
5. Crystalline eye lens present; urosome segment 1 with a prominent dorsal keel ..... *holbolli* (Krøyer) (p. 106)  
Crystalline eye lens not present; urosome segment 1 dorsally smooth ..... 6
6. Gnathopod 2, dactyl distinctly shorter than palm ..... 7  
Gnathopod 2, dactyl equal to palm ..... 10
7. Peraeopod 7, posterior margin of segment 2 (basis) strongly tapered distally ..... *pacificus* Gurjanova  
Peraeopod 7, posterior margin of basis weakly or not tapered distally ..... 8
8. Gnathopod 1, segment 6 (propod) broadened distally; peraeopods 5, 6 and 7, posterior marginal serrations of basis without setae ..... *eous* Gurjanova  
Gnathopod 1, segment 6 not broadened distally; peraeopods 5, 6 and 7, posterior proximal serrations of basis each with inserted seta ..... 9
9. Gnathopod 2, segment 5 twice as long as segment 6; telson elongate, twice as long as broad ..... *granulosus* Gurjanova (p. 111)  
Gnathopod 2, segment 5 less than twice as long as segment 6; telson of medium length, less than twice width ..... *tenax* Barnard
10. Uropod 3, rami broad, margins parallel, tapered only at tip ..... *punctatus* Gurjanova  
Uropod 3, rami slender, margins gradually tapered distally ..... 11
11. Peraeopods 5, 6 and 7, serrations of posterior margins of basis without setae ..... *propinquus* Sars  
Peraeopods 5, 6, and 7, posterior marginal serrations of basis with inserted setae ..... 12
12. Peraeopod 4, segment 5, posterior margin with 3 strong spines; uropod 2, peduncle and rami spinose ..... *subrobustus* Hurley  
Peraeopod 4, segment 5, posterior margin lacking spines; uropod 2, peduncle and rami smooth ..... *zetesimus* Hurley

## *Hippomedon holbolli* (Krøyer, 1846)

### Figure 1

*Anonyx holbolli* Krøyer, 1846, t. 15, fig. 1 a-s

### *Hippomedon holbolli*

— Sars, 1895, p. 58, pl. 21 no. 2

— Stebbing, 1906, p. 58

— Gurjanova, 1951, p. 229

— Gurjanova, 1962, p. 104, fig. 93

**Material examined:** 10 samples, 40 specimens. Greenland, various coll., 1900 to 1933; Pearyland, North Greenland, 4 June 1966, 105 m; Murchison Sound (77°31.6'N, 70°40'W), 24 August 1968, 50 m; northwestern Greenland

(75°53.5'N, 66°29.7'W), 8 August 1980, 72 m, J. Just coll.; Beaufort Sea (70°33'N, 145°40'W), 9 August 1972, 50 m, R/V Glacier, Department of Oceanography, Oregon State University coll.; 70°13'N, 140°50'W, 4 April 1914, stomach contents of seal, F. Johansen coll.

**Diagnosis:** Female ovig. 18.0 mm, Beaufort Sea. Body integument with distinct surface striations. Eyelobe not developed. Eyes with a crystalline lens; crimson pigment in the eye region which is visible in live specimens, disappearing quickly in preservative. Antenna 1, flagellum 12-segmented, basal segments fused, segment 1

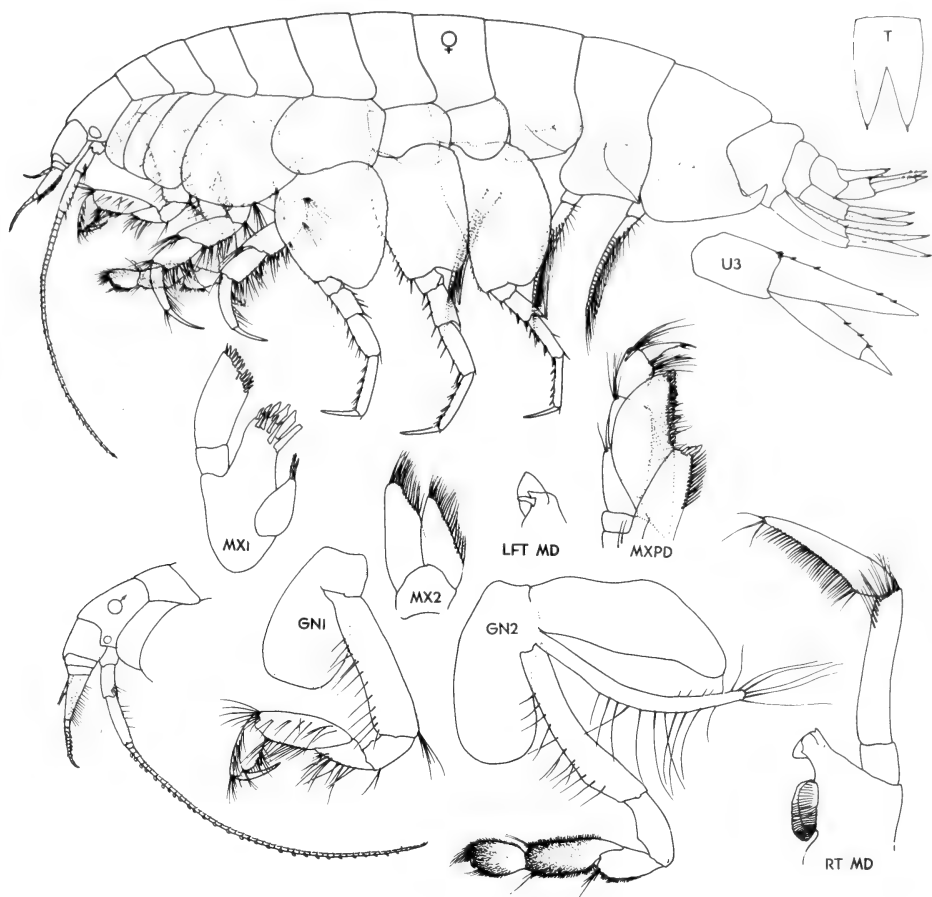


Figure 1. *Hippomedon holbolli* (Krøyer) Beaufort Sea ♀ ov., 18.0 mm.

and 2 each bearing a strong posterodistal spine; accessory flagellum 5-segmented. Antenna 2, peduncular segment 5 slender; flagellum approximately 45-segmented. Mandibular palp, segment 3 slightly shorter than segment 2, strongly tapered distally, inner margin with a dense setal row. Maxilla 1, inner plate with 2 distal setae. Gnathopod 1, segment 6, palmar margin oblique, convex, subequal to posterior margin. Gnathopod 2, segment 5 not distally bulbous; dactyl shorter than palm. Peraeopods 3 and 4, segments 4, 5 and 6, posterior margin lined with many strong spine groups. Epimeral sideplate 3 posterodistal tooth moderately stout, upturned. Urosome segment 1 dorsally with a depression followed by

a rounded crest. Uropod 1, peduncle and rami with numerous short outer marginal spines. Uropod 2, margins with few short spines. Uropod 3, margins of rami non-plumose, with short spines only. Telson lobes fused in basal  $\frac{1}{3}$ , apex with notch and single small spine.

Male. 15.0 mm, Beaufort Sea. Antenna 1 slightly longer than in female, 16-segmented. Antenna 2 much longer than in female, approximately 70-segmented.

*Remarks:* Specimens from the Beaufort Sea are very similar to those from Greenland. In large males (15 mm) from Greenland, peduncular segments 4 and 5 are armed anteriorly with numerous brush setae. In seal stomach contents

from the Beaufort Sea, brush setae could not be seen on smaller males although calceoli were visible. Uropod 3 exhibits slight variation in the rami; in Greenland material the rami are slightly more broadly lanceolate than in specimens from elsewhere.

**Distributional ecology:** A widely distributed circumpolar species; in the Pacific Ocean, extending possibly (but not authentically) into the northern part of the Bering Sea.

***Hippomedon denticulatus* (Bate)**

Figure 2

*Anonyx denticulata* Bate, 1857, p. 139

*Hippomedon denticulatus*

- Sars, 1895, p. 56, pl. 20
- Stebbing, 1906, p. 59
- Chevreux & Fage, 1925, p. 53, fig. 37
- Gurjanova, 1955, p. 233, fig. 96
- Gurjanova, 1962, p. 106, fig. 23

— Lincoln, 1979, p. 75, fig. 28

*Non Hippomedon denticulatus*

— Barnard, 1954, p. 4, pl. 2-3

— Barnard, 1964b, p. 80

— Barnard, 1971 (forma *subrobustus* Hurley (from Oregon) p. 28, figs. 17-18

— Barnard, 1971 (*propinquus* shelf form of California) p. 30, fig. 193-m

— Barnard, 1971 (form with gaped gnathopod 2) p. 31, fig. 21

— Barnard, 1971 (*propinquus* of north-western Atlantic Ocean) p. 31, fig. 20

*Non Hippomedon denticulatus orientalis* Gurjanova, 1962, p. 104, fig. 22.

*Non Hippomedon denticulatus orientalis* Gurjanova (off Alaska) = Barnard, 1971 p. 30, fig. 19 a-d.

*Non Hippomedon denticulatus* — Hurley, 1963, p. 137, fig. 45

**Material examined:** 2 samples, approximately

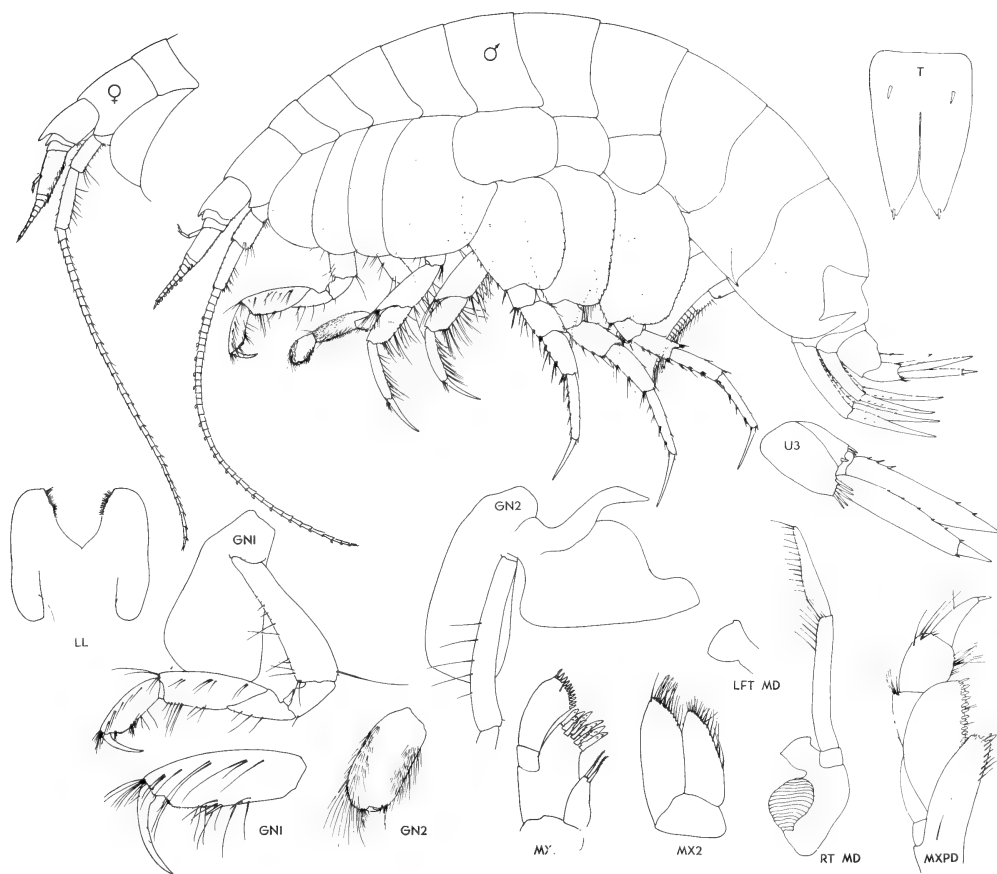


Figure 2. *Hippomedon denticulatus* (Bate) Thor. I., Skaggerak ♂ 11.0 mm, ♀ 9.5 mm.

50 specimens, Skagerrak, 6 March 1903, 140 m. S.C. Johansen coll.; 28 October 1904, 44 m.

**Description:** Male 11.0 mm. Eyelobe small, acute. Eyes narrow, linear, slightly widened below, pigment (in life) light red with a few opaque white stripes horizontally. Antenna 1, peduncular segments 1 and 2 each produced strongly anterodistally into an acute process. Flagellum 11-segmented, first fused segments and article 1 with a sharp spine posteriorly; accessory flagellum 3-segmented. Antenna 2, peduncular segments 3-5 with brush setae anteriorly and a few long setae posteriorly; flagellum 41-segmented. Mandibular palp segments slender, segment 3 distinctly shorter than 2, inner marginal setae sparse. Maxilla 1, inner plate with 2 apical setae. Gnathopod 1, coxal plate broadened distally, distal margin nearly straight; segment 6 slender, untapered; palm oblique, about equal to posterior margin, defined by one palmar spine. Gnathopod 2, segment 6, palm short, transverse, dactyl equal to palm. Peraeopods 3 and 4, segments 4, 5 and 6, posterior margins with slender spine tufts; segment 4 produced anterodistally, dactyl long and thin. Epimeral plate 3, hind margin produced into a long, slender, well-tapered tooth with a distinct dorsal notch. Uropod 3, rami long, slender, sparsely spinose. Telson lobes fused basally, inner margins proximally parallel, distally diverging, apices with one spine.

Female (ov.) 8 mm. Antenna 1, flagellum 9-segmented; antenna 2, flagellum 33-segmented.

**Remarks:** Sars (1895) figured males in which antenna 1 was both long and short. All male specimens from the Skagerrak examined here had short antenna 1.

Barnard (1964b) opined that *H. propinquus* Sars and *H. denticulatus* (Bate) are not specifically distinct; rather that *H. propinquus* is a juvenile stage of the latter in which the dorsal notch of the third epimeral plate and the anterodistal process of the first two segments of antenna 1 have not yet reached the sexually mature form. Barnard (1971), further elaborated this view, with particular attention to the epimeral notch. He interpreted some small (5-6 mm) sexually mature specimens from California and Oregon that lacked an epimeral 3 notch to be a dwarf southern race of *H. denticulatus*. He identified mature specimens (larger than 5 mm) with a notch from California and Oregon as various forms of *H. denticulatus*, whereas those

specimens lacking a notch he designated as a "propinquus" phase. Barnard concluded that *Hippomedon* populations from Oregon and California form a complex of phenotypes of a single species which could ultimately be linked to *H. denticulatus orientalis* Gurjanova, 1962 of the far eastern seas of the USSR.

In addition to *H. denticulatus*, a notch on epimeron 3 has been described in five other species, viz., *H. coecus* Holmes, *H. reticulatus* Stephensen, *H. massiliensis* Bellan-Santini, *H. mercatoris* Pirlot, and *H. denticulatus orientalis* Gurjanova. *H. denticulatus orientalis* was designated a subspecies by Gurjanova (1962); however, this form is morphologically distinct from the type species in many species-significant characters of the overall body, eyes, antenna 1, gnathopod 1, uropod 3, and telson and merits full species status.

In juvenile and adult specimens (6.0 mm to 11.0 mm) of both *H. denticulatus* and *H. propinquus* from the Skagerrak, characters which separate these species as adults were equally applicable in the juvenile stage. Thus, in smallest specimens of *H. denticulatus* (6.0 mm) the pronounced first antennal anterodistal process is distinct; moreover, the third epimeral tooth is long and slender, with a distinct dorsal notch, and quite unlike that of *H. propinquus* of comparable size. Such well defined "mature" characters of specimens 6 mm in body length cannot be growth-dependent, thereby confirming their value in species identification. These two species are separated by characters given in the key and in the text, notably by the first coxa which, in *H. denticulatus*, is maximally expanded at the flattened distal margin.

Other species from the northwest Pacific that bear an epimeral notch (e.g., *H. columbianus* n.sp.) are also found to be morphologically distinct from Atlantic material of *H. denticulatus* and *H. propinquus* (see also p. 111).

### *Hippomedon columbianus* n.sp.

Figure 3.

*Hippomedon denticulatus* Barnard, 1954, p. 4, pl. 2, 3

Barnard, 1971, p. 31-34, fig. 21 (form with gaped gnathopod 2)

Hurley, 1963, p. 137-140, fig. 45

**Material examined:** 36 specimens from 18 samples. British Columbia: Swanson Bay stns., J (53°0.58'N, 128°30.6'W) 67 m, 4 April 1973,

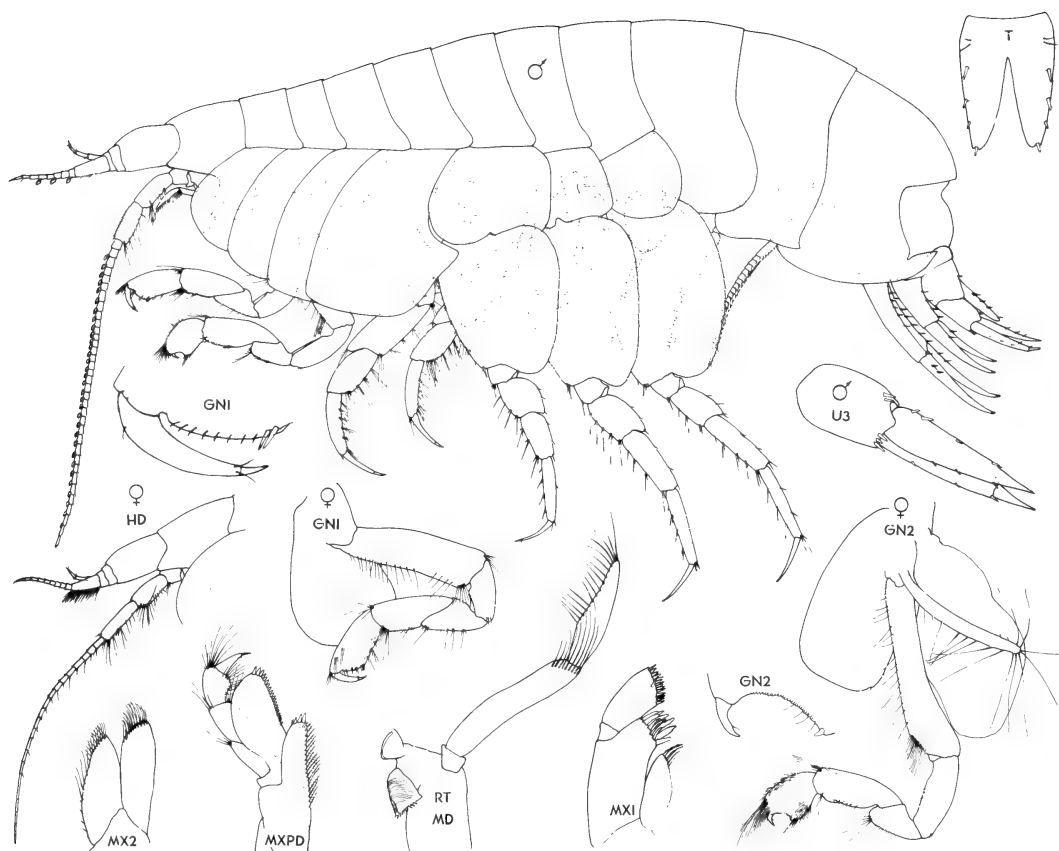


Figure 3. *Hippomedon columbianus* n.sp. ♂ 7 mm 51B-029 Sta. J. Swanson Bay, B.C.

holotype male (7 mm figd. NMC-C-1981-1051), allotype female ov. (8 mm figd. NMC-C-1981-1052), NMNS slide mounts, paratype male imm., 3 juvs. NMC-C-1981-1053; (53°0.76'N, 128°30.05'W) 45-47 m, 18 November 1975, C. Levings coll.; Verdier Pt., Saanich Inlet (48°22.5'N, 123°29'W) 4-7 m, 19 March, 1 May 1975, K. Conlan, coll.; French Creek, north of Nanaimo (49°20'N, 124°25'W), 23 August 1977, P. O'Rourke coll.; B14 Trevor Channel (48°48.9'N, 125°11'W) 40-50 m, 25 May 1977, E.L. Bousfield coll.; W5-B, McCauley Pt., (53°50', 130°20'W) 55 m, 26 August 1976, G. O'Connell coll.; Vancouver Harbour (49°18'N, 123°12'W), 17 June 1976, C. Levings coll.

**Diagnosis:** Male holotype (7 mm). Eyelobe moderately deep, subacute. Eye not visible in preserved specimens. Antenna 1, peduncular segment 2 with 1 large sensory seta distally; main flagellum 10-segmented, segment 1 equal to first

two segments of 3-segmented accessory flagellum. Antenna 2, peduncular segment 4 with 10, 5 with 14 short setal tufts anteriorly, long seta posteriorly; flagellum 38-segmented. Antennae calceolate. Mandible palp segment 3, setae on medial margin not dense. Maxilla 1, inner plate with 4 apical plumose setae. Maxilla 2, inner plate broadened basally. Gnathopod 1, coxa expanded distally; segment 6 slightly expanded distally, setal groups on posterior margin and medio-distally; palm oblique, distinctly shorter than posterior margin of hand, dactyl hooded. Gnathopod 2 segment 6 slightly expanded distally, dactyl much shorter than concave palm. Peraeopods 3 and 4, segments 4, 5 and 6 with long, slender spine groups posteriorly. Peraeopods 5, 6 and 7, segment 2 weakly serrate posteriorly; segments 4, 5 and 6, anterior margins 3-5 spine groups; posterior margins with a few short spines. Epimeral sideplate 3 with a short



notch dorsally over a medium-sized tooth. Urosome 1 with dorsal depression. Uropod 1, peduncle lateral margin bearing 6-7 spines, medial margin 9-10, margins of rami sparsely spinose proximally. Uropod 2 peduncle with 4-5 spines, rami 1 or 2 each. Uropod 3 each ramus bearing 2 or 3 short marginal spines. Telson with 3 to 4 pairs of dorsal spines, apices notched, each with one spine.

Female allotype 8.0 mm ovigerous. Antenna 2, flagellum shorter than male, 22-segmented.

**Distributional ecology:** *H. columbianus* has been collected from the middle and southern mainland coasts of British Columbia, and the inner and outer coasts of southern Vancouver Island in depths of 4 m to 67 m. Ovigerous females were present in samples taken in March, April, May and August.

**Remarks:** In *H. columbianus* specimens, the epimeral notch is not visible at 2.0 mm, barely visible at 3.0 mm to 4.0 mm, and easily visible at 5.0 mm.

*H. columbianus* differs from Atlantic *H. denticulatus* in lacking a pronounced anterodistal process on the peduncle of antenna 1, and the third epimeral tooth is shorter and stouter, with a smaller notch. It differs from both *H. denticulatus* and *H. propinquus* in the smaller relative length of segments 5 and 6, the shorter and less oblique palm of gnathopod 1, and in the presence of 4, not 2, apical setae on the inner plate of maxilla 1.

From the North Pacific species, *H. subrobustus* Hurley and *H. zetesimus* Hurley, *H. columbianus* is separable primarily by its third epimeral notch; moreover, its telson is shorter, with broader lobes than that in *H. subrobustus*, and segment 6 of gnathopod 1, the coxal plate of pereopod 4, and the spination of uropod 2 differ from Hurley's figures of *H. zetesimus*. The rather slender tapering rami of the third uropods, and the long palm of gnathopod 2 distinguish *H. columbianus* from *H. orientalis* Gurjanova.

The third epimeral notch, visible in specimens 5 mm and larger, as well as the long palm of gnathopod 2, separate *H. columbianus* from *H. denticulatus* (f. *subrobustus*), (Barnard, 1971), and from *H. denticulatus* (*propinquus* shelf form) (Barnard, 1971). *H. columbianus* is possibly synonymous with *H. denticulatus* (Barnard, 1954), *H. denticulatus* (form with gaped gnathopod 2) (Barnard, 1971), and *H. denticulatus* (Hurley,

1963). Although corresponding specimens have not been examined, the figures and descriptions agree reasonably closely with *H. columbianus*.

### *Hippomedon granulosus* Bulychева, 1955

Figure 4.

*Hippomedon granulosus* Bulychева 1955, p. 195, fig. 2.

*Hippomedon granulosus* Gurjanova 1962, p. 123, fig. 31.

**Material examined:** Two samples, 2 specimens. St. Lawrence Is., Bering Sea (64°N, 169°W), 1 July 1980, 40 m; 10 July 1980, 30 m, coll. J. Oliver.

**Diagnosis:** Female ov. (13 mm). Eyelobe moderate, subacute. Eyes not visible in preserved material. Antenna 1, anterodistal processes of peduncular articles 1 and 2 moderate; main flagellum 10-segmented; conjoint segments equal to first 2 segments of 3-segmented accessory flagellum. Antenna 2, peduncular segment 5 distinctly longer than segment 4, flagellum 25-segmented. Mandibular palp, segment 3 strongly tapered distally, not markedly shorter than segment 2. Maxilla 1, inner plate with 3 apical setae. Maxilliped outer plate densely toothed on the inner margin. Gnathopod 1, article 6, palm oblique, distinctly shorter than posterior margin of hand, defined by two palmar spines; dactyl slightly longer than palm. Gnathopod 2 segment 6 short, broad; palmar margin long, concave; dactyl considerably shorter than palm. Pereopods 3 and 4, posterior margins of segments 4, 5 and 6 lined with long slender spines. Pereopods 6 and 7, segment 2 barely tapered distally, posterior margins serrate, notches with short setae. Posterodistal tooth of epimeral plate 3 large, acute. Uropod 3, rami elongate, strongly tapered distally, 2 to 3 short spines on the outer margin. Telson lobes fused basally, long, well tapered, blunt distally, apices each with 3 small, unequal spines.

**Distributional ecology:** Gurjanova (1962) recorded this species from the Sea of Japan and the Sea of Okhotsk at depths of 60 m to 134 m. The samples from gray whale feeding pits, northeast of St. Lawrence Island at a depth of 25 m are the first records of *H. granulosus* from the north Bering Sea.

**Remarks:** Present specimens differ from those of Gurjanova (1962) in being larger (to 13 mm vs. 10 mm), possessing a few small spines on the

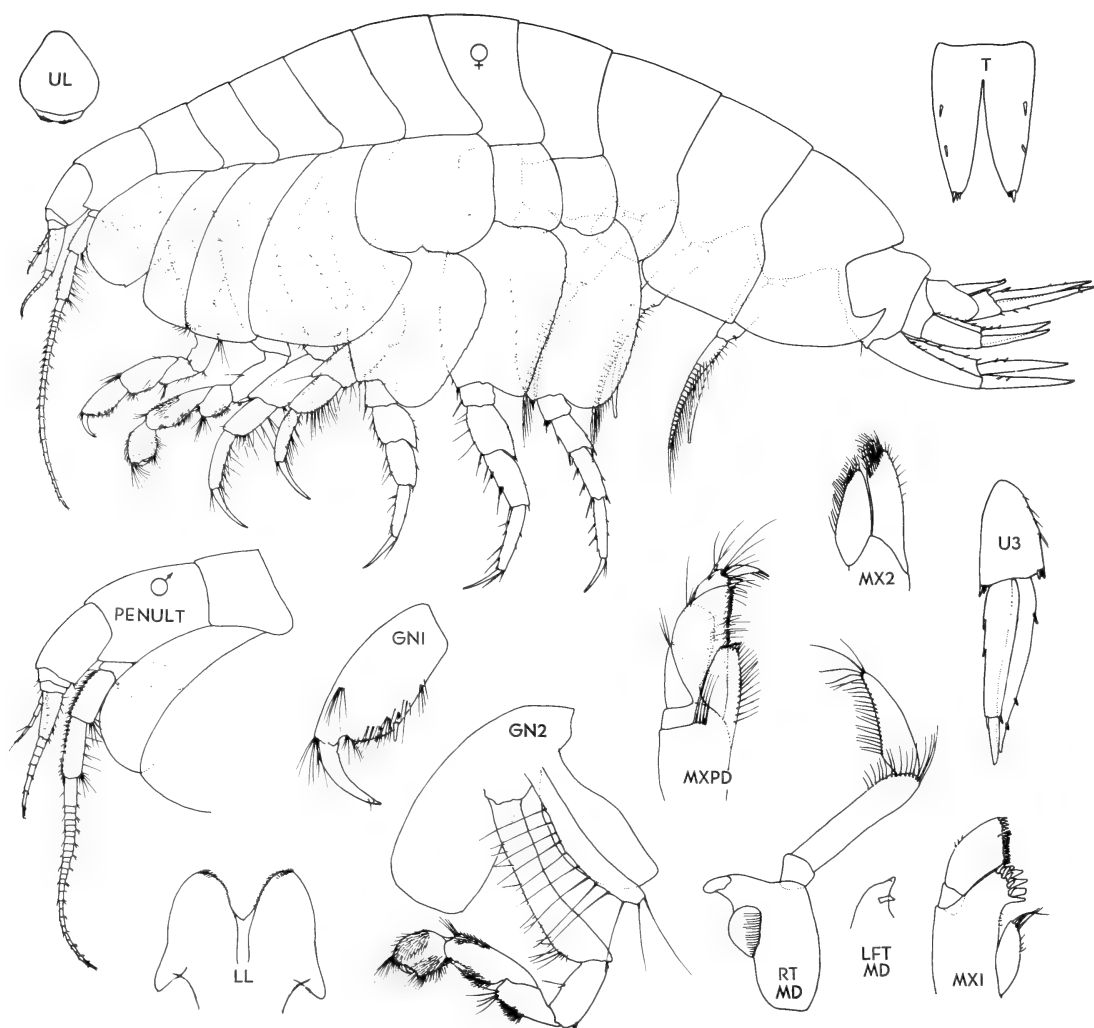


Figure 4. *Hippomedon granulosus* Bulycheva. St. Lawrence I. Bering Sea. ♀ ov., 13.0 mm., ♂ penult. 9.0 mm.

rami of uropod 3 versus none in the type, and having three apical spines on the telson lobes versus two in Gurjanova's specimens.

#### *Hippomedon* species indeterminate

The following regional taxonomic entities recorded in the literature could not be critically evaluated because specimens were unavailable for examination, and the original descriptive commentary and illustrations were too limited. These include three forms of *H. denticulatus* from Pacific coastal regions described by Barnard (1977), viz. *H. denticulatus* (f. *subrobustus* Hurley) from Oregon; *H. d. orientalis* Gurjanova

from Alaska; and *H. d. (propinquus* shelf form) from California. As outlined previously (p. 109) all Pacific *denticulatus*-like forms are herewith considered distinct from the Atlantic species, *H. denticulatus*. Barnard's figures of *H. denticulatus* f. *subrobustus* differ from *H. subrobustus* Hurley in the following respects: antenna 2, ped. segment 5 is distinctly longer than 4 rather than subequal, peraeopod 5, segment 6 is longer with more spines anteriorly; uropod 3, terminal segment of outer ramus is much shorter; and the telson is shorter and broader with 2 apical spines per lobe.

*H. denticulatus orientalis* Gurjanova from

Alaska as described by Barnard (1971) differs from *H. denticulatus orientalis* Gurjanova (1962) from the U.S.S.R. in the following respects; segment 6 of gnathopod 1 has parallel sides; segment 6 of gnathopod 2 is barely expanded; the distal lobes of coxa 5 are almost equal; segment 2 of peraeopod 6 is slightly tapered distally; and segment 6 of peraeopods 6 and 7 have 1 or 2 spines posteriorly. And finally, figures of *H. denticulatus* (*propinquus* shelf form) differ significantly from Atlantic specimens in the form of gnathopod 1, especially the expanded coxa, subequal segments 5 and 6, shorter palm, and presence of two spines, and the posterior tooth of epimeral plate 3 has a small dorsal notch. These forms are all distinct from North Pacific species treated herewith and in other papers. Precise taxonomic placement of these three forms awaits re-examination of the original material, and more extensive series of specimens.

***Wecomedon* new genus**

**Diagnosis:** Body elongate, moderately deep. Head small, partially hidden by coxa 1; anterior head lobe small to moderate, variable. Eyes whitish in preserved specimens, moderately large, oval, slightly widened below. Coxal plates 1-4 very deep; coxa 4 weakly serrate on the posterodistal margin. Epimeral plate 3 produced posterodistally into an upturned tooth. Antenna 1 moderately short; segment 1, moderate to long, weakly inflated, slightly produced anterodistally; segments 2 and 3 not strongly telescoped into 1; flagellum proximal segments normal, not fused; non-calceolate. Antenna 2 slightly longer than antenna 1 in the female, elongate and occasionally calceolate in the male. Mandible, palp, segment 1, distal setae few or lacking;

segment 3 more than 1/2 segment 2, medial margin comb-setose, remaining surfaces sparsely setose. Maxilla 1, palp densely toothed distally; outer plate with eleven pectinate spines; inner plate with 2 to 5 apical setae. Maxilliped, inner margin of inner plate setose; outer plate extends distad of palp segment 2, inner margin closely spinose. Gnathopod 1 segment 5 longer than 6; segment 6 long, narrow, palm slightly oblique, distinctly shorter than posterior margin; dactyl strong. Gnathopod 2 minutely subchelate. Peraeopods 3 and 4, segments 4, 5 and 6, posterior margins with slender spine tufts. Peraeopods 5, 6 and 7 unequal, 5 distinctly shortest, 6 longest; coxal plate of 5 as deep as anterior margin of segment 2; segment 4 moderately expanded. Paraeopod 6 segment 2 broad, untapered; peraeopod 7 very broad, weakly or not tapered distally, posterodistal margin straight. Peraeopods 2, 3 and 4 with simple, non-lobate gills, peraeopod 5 coxal gill with one long, slender accessory lobe, peraeopod 6 gill with 3 short accessory lobes, peraeopod 7, gill lacking. Uropod 3 rami subequal, lanceolate, margins spinose, setose in male, sometimes setose in female. Telson lobes broad, weakly tapered, truncate apically, each bearing 2-5 spines (rarely 1).

**Etymology:** A combining form of *Hippomedon* and *wecomus* the type species.

**Type species:** *Hippomedon wecomus* Barnard 1971.

**Additional species:**

- Wecomedon similis* new species
- W. wirketis* (Gurjanova) 1962
- W. boreopacificus* (Gurjanova) 1962
- W. minusculus* (Gurjanova) 1938

**Key to Species of *Wecomedon***

- 1. Uropod 3, outer ramus, segment 2 longer than 1/2 segment 1; telson lobes, apices blunt, each with one large thick spine ..... *W. minusculus* (Gurjanova)
- Uropod 3, outer ramus, segment 2 less than 1/2 segment 1; telson lobes apices truncate, each with more than one medium spine ..... 2
- 2. Anterior head-lobe long, narrow, acute; uropod 3, outer ramus, outer margin with 4 or fewer single spines ..... 3
- Anterior head-lobe short, stout, subacute; uropod 3, outer ramus, outer margin with more than 4 single spines, proximal spines often in groups ..... 4
- 3. Gnathopod 1, segment 6, palm defined by two large locking spines; telson lobes relatively short, broad, fused basally 1/3 ..... *W. wirketis* (Gurjanova) (p. 116)
- Gnathopod 1, segment 6, palm indistinct, locking spines lacking; telson lobes elongate, length nearly 3 times width, fused basally 1/4 ..... *W. boreopacificus* (Gurjanova) (p. 118)

4. Gnathopod 1, segment 2, anterior margin strongly setose; antenna 1 and 2 (♀) subequal; epimeral plate 3 posterodistal tooth, long, slender ..... *W. similis* n.sp. (p. 115)  
 Gnathopod 1, segment 2, anterior margin sparsely setose; antenna 2 (♀); distinctly (25%) longer than antenna 1; epimeral plate 3, posterodistal tooth, short, stout .....  
 ..... *W. wecomus* Barnard (p. 114)

*Wecomedon wecomus* (Barnard, 1971)

Figure 5.

*Hippomedon wecomus* Barnard, 1971,  
 p. 37, figs. 24-25

**Material examined:** 53 specimens from 14 samples. Alaska: Bousfield stn. 1980, S11 Lisianski Strait, (58°06.4'N, 136°27'W), 3 to 10 m., S18 Kamenoi Pt., Kruzof Is., (55°08'N, 135°34'W), 2 to 7 m, 2 August 1980. British Columbia, Vancouver Island: Bousfield stn., 1959, V22 Oyster Bay (49°55'N, 125°11'W), intertidal; 1975, P22 Trevor Channel (48°49'N, 125°12.5'W) 27.5 m; 1976, B22 Dodger Channel (48°50.4'N, 125°12.1'W), 18 m; 1977, B18 Trevor Channel (48°48.8', 125°

13.5'W) 36 m, B21 off Brady's Beach (48°50.2'N, 125°08.5'W) 18-28 m.

Washington, USA: Bousfield stn. 1966, W35 Agate Beach Clallam Co., (48°15'N, 124°16'W) intertidal.

**Description:** Female (10.0 mm). Eyes vertically ovate, bright red in life, indistinct in preserved specimens. Antenna 1, peduncular segment 1 long, weakly inflated; flagellum 17-segmented; accessory flagellum 4-segmented. Antenna 2 slightly longer than antenna 1; peduncular segment 3 with long setae medio-distally, segment 4 setose posterodistally; segment 5 slightly longer than 4 with long setal tufts posteriorly; flagellum about 20-segmented.

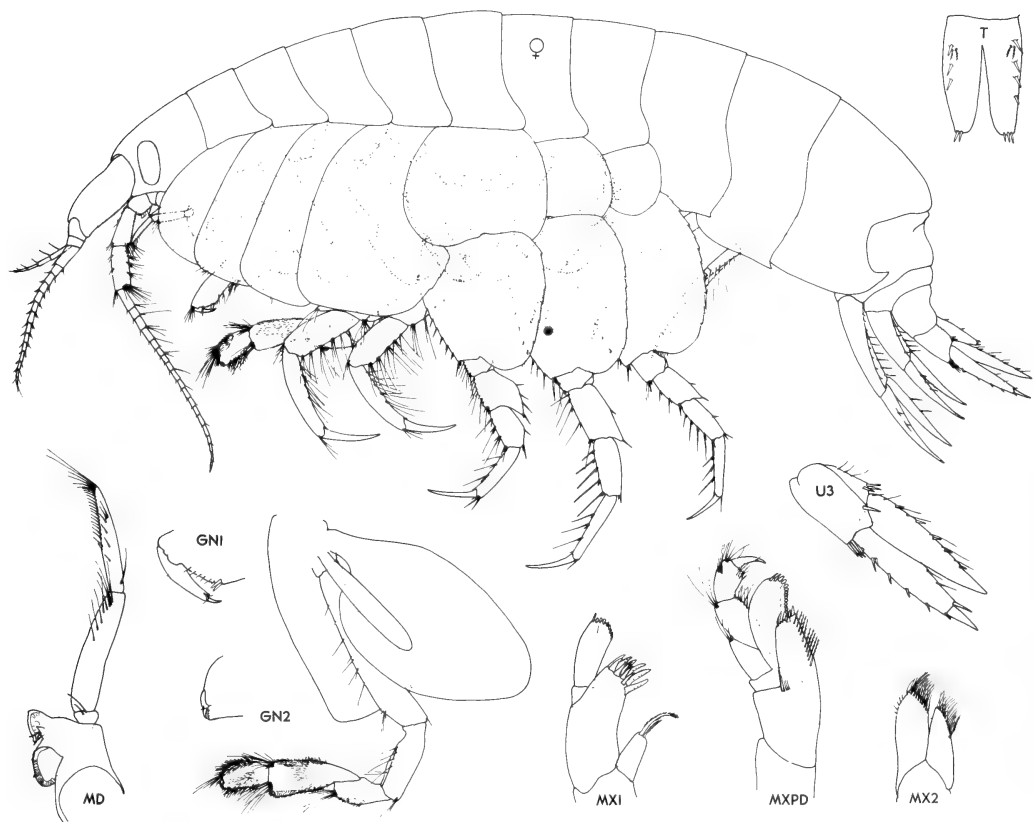


Figure 5. *Wecomedon wecomus* (Barnard) ♀ br. II, 10 mm, Stn. B27, Dodger Channel, V.I., B.C.

Mandible, palp segment 1 with 2 short distal setae. Maxilla 1, inner plate with 2 apical setae. Gnathopod 1, anterior margin of segment 2 sparsely setose; segment 6 typical, weak setal tufts on margins. Peraeopods 5 and 7, segments 4 and 5 subequal in length, segment 4 of peraeopod 5 as broad as long; peraeopod 6 segment 4 slightly longer than 5. Posterodistal tooth of epimeral plate 3 short, stout. Urosome segment 1 with a weak saddle-shaped, mid-dorsal depression. Uropods 1 and 2, peduncles spinose, rami weakly spinose. Uropod 3 outer margins of rami strongly spinose, inner margins weakly setose. Telson lobes relatively long, dorsolaterally with 2-3 pairs of spines, apices each with 3 strong spines.

Male (penultimate instar) 10.0 mm. Antenna 2 flagellum 40-segmented, non-calceolate.

*Distributional ecology*: Present material

ranges from southeastern Alaska, where its distribution overlaps with *W. similis*, to Oregon in sandy shallows, lower intertidal to depths of 28 m (52-100 m Barnard, 1971). No ovigerous females were present in the material studied, (June-August).

*Remarks*: The subadult female (10 mm) figured here agrees well with small specimens (6.8 mm) figured by Barnard (1971). Larger specimens (13 mm) possess longer antennae, a more setose mandibular palp, more strongly toothed maxilliped outer plate, more heavily setose rami of uropod 3, and more dorsally spinose telson lobes.

*Wecomedon similis* n.sp.

Figure 6.

*Material examined*: 21 specimens from 10 samples. Alaska stns.; St. Lawrence Island

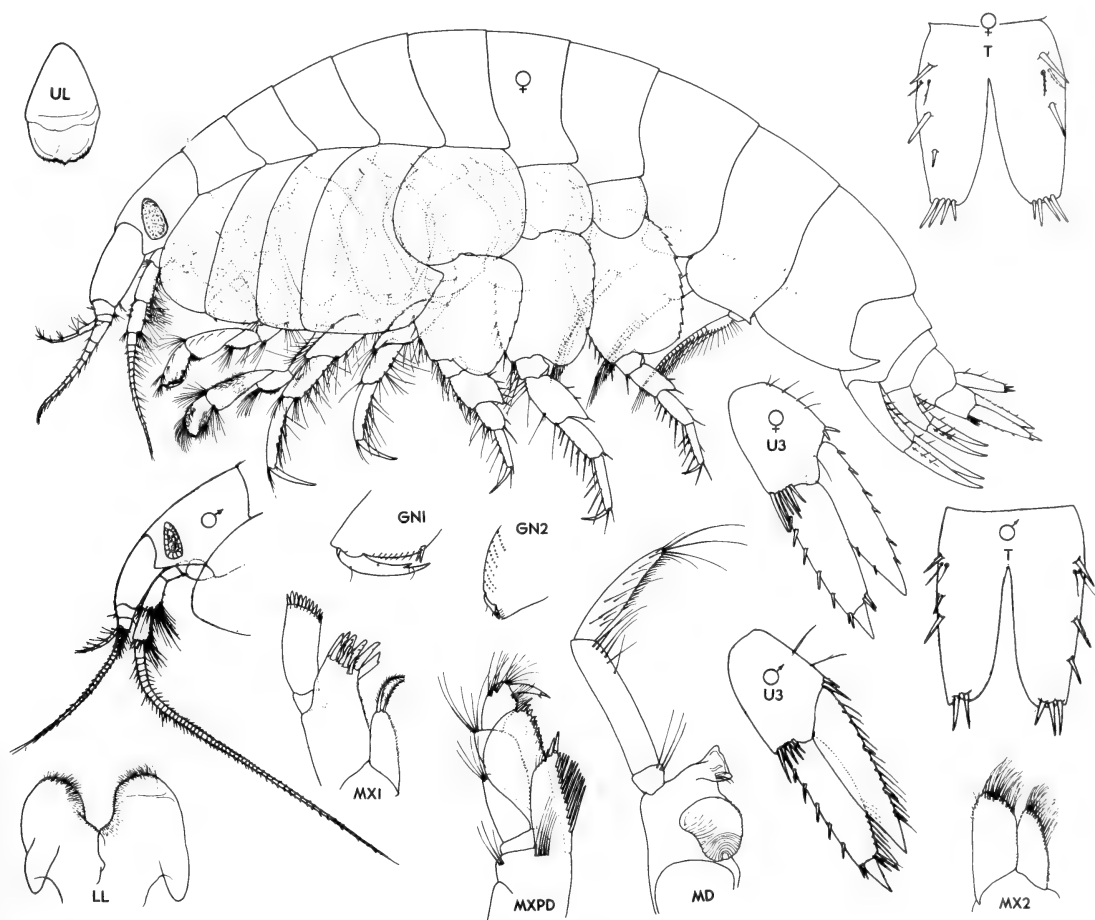


Figure 6. *Wecomedon similis* n.sp. Stn. H13, Lelu I., B.C. ♀ 11 mm. ♂ 10 mm.

1965, whale stomach contents, G. Pike, coll. Bering Sea, St. Lawrence Is., (64°N169°W) 13 m and 29 m, 10 July 1980, J. Oliver coll. North central coastal British Columbia: Bousfield stn. H 31 Lelu Island (54°21'N, 130°18'W), intertidal, fine, dark, sand flats, 14 July 1964, holotype female (11.0 mm figd. NMC-C-1981-1054), allotype male, penultimate (10.0 mm), NMC-C-1981-1055 NMNS slide mounts; 2 paratype imm. females, NMC-C-1981-1056.

**Diagnosis:** Female holotype 11.0 mm. Eyelobe short, rather broad. Eyes oval, indistinct in preserved specimens. Antennae about equal in length. Antenna 1, peduncular segment 1 long, cylindrical; flagellum 14-segmented; accessory flagellum 4.5 segmented. Antenna 2, peduncular segment 3 setose mediodistally; segment 4 setose posterodistally; segment 5 slightly shorter than 4, bearing tufts of long setae posteriorly; flagellum 18-segmented, each segment with long posterodistal setal tuft. Mandible, segment 1 of palp with a long setal tuft distally. Maxilla 1, inner plate with 2 apical setae. Maxilliped, outer plate almost reaching segment 3 of palp. Gnathopod 1 anterior margin of segment 2 densely setose, segment 6 typical, setal tufts on the anterior and posterior margins. Gnathopod 2, segment 5 well expanded distally with a prominent posterodistal "cushion"; segment 6 untapered distally. Peraeopods 5 and 6, segment 4 slightly longer than 5; peraeopod 7 segments 4 and 5 subequal. Epimeral plate 3 posterodistal tooth moderately long and slender. Uropod 1, peduncle outer margin with 6-8 long spines, inner margin with 6 to 7 shorter spines; rami with 2 and 3 spines proximally. Uropod 2 peduncle outer margin with 4 to 5 spines; rami with 3 and 1 marginal spines. Uropod 3, peduncle with 6-10 strong spines distally; rami broadly lanceolate, outer margins with 5 to 6 spines, inner margins 0 to few spines. Telson lobes relatively short, broad, each bearing 2 to 4 strong apical spines, and 3 to 4 dorsal spines.

Male allotype. (penultimate instar 10.0 mm). Antenna 1, flagellum 21-segmented. Antenna 2 flagellum 46-segmented. Uropod 3, rami spinose, inner margins setose.

**Distributional ecology:** *W. similis* was present in samples from the North Bering Sea, south to the north-central coast of British Columbia, bathymetrically from intertidal sand flats to depths of 29 m. No ovigerous females present.

**Remarks:** Material from the Bering Sea (received after types had been designated and figured) contained larger, more mature specimens. The largest female (19.0 mm) agrees with the figured specimen in most respects. The body parts are more strongly developed, the armature of spines and setae more prominent, but the number of apical spines on the telson are fewer (3-4). Of two mature males, one (16.0 mm) had three calceoli on the second antenna, while the other (14.0 mm) had none. Antennal calceoli may be in the process of reduction and/or loss within members of the genus.

Differences noted between the sibling species *W. similis* and *W. wecomus* (Barnard) are slight. *W. similis* is somewhat larger, more setose, and more northerly in distribution. It is distinguished by the moderately long, slender epimeral tooth, by the subequal antenna (females), and by the lack of a dorsal depression of urosome 1 (present in *W. wecomus*). Both species are larger than *W. minusculus* Gurjanova. This western Pacific species also has a shortened segment 5 of gnathopod 2, and a longer terminal segment of the outer ramus of the third uropod.

***Wecomedon wirketis* (Gurjanova, 1962)**

Figure 7.

*Hippomedon wirketis* Gurjanova, 1962, p. 115, figs. 28a, 28b.

**Material examined:** 2 samples, 11 specimens. Bering Sea, northeast of St. Lawrence Is., (64°N, 169°W), July 1980, J. Oliver coll.

**Diagnosis:** Female ov. (18.0 mm). Anterior head lobe narrow, sharp; inferior antennal sinus distinct, bounded behind by cusp. Eyes moderate, indistinct in preserved specimens. Antenna 1, peduncular segment 1 moderately long; flagellum 15 segmented; accessory flagellum 4½ segmented. Antenna 2 slightly longer than antenna 1; peduncular segment 3 with mediodistal setal tuft; segment 4 shorter, broader than 5, posterior margin weakly setose and posterodistally with tuft of long setae; segment 5, posterior margin with several setal tufts; flagellum 27 segmented, proximal segments with posterodistal setal tufts. Mandible, palp, segment 1 lacking setae. Maxilla 1, inner plate with 4 or 5 apical setae. Maxilliped, outer plate large, almost reaching distal end palp segment 3; inner marginal teeth present distally, reduced in size proximally. Gnathopod 1, segment 2 setose anteriorly; segment 6 palm oblique, strongly defined by

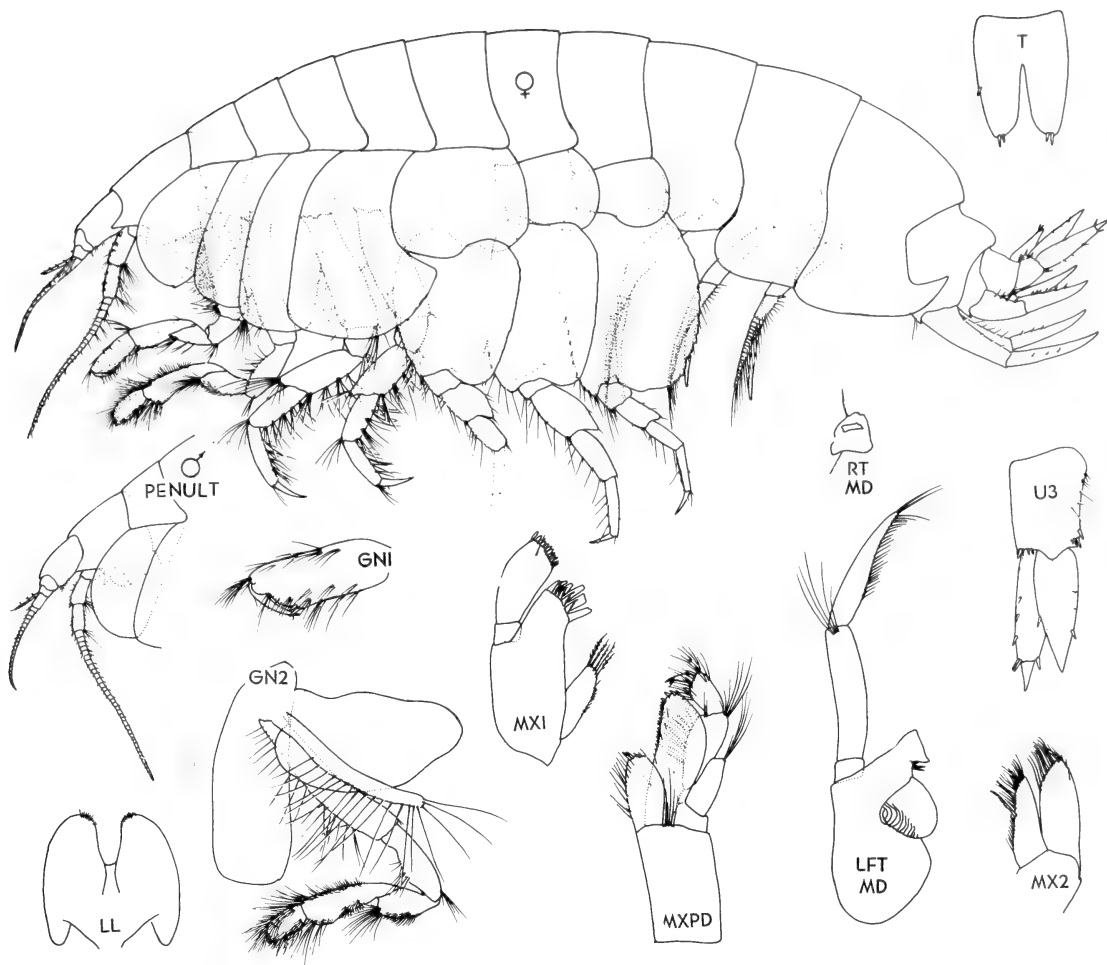


Figure 7. *Wecomedon wirketis* (Gurjanova) St. Lawrence I., Bering Sea. ♀ ov. 18.0 mm., ♂ penult. 13.0 mm.

two locking spines, strongly setose anterior and posterior margins. Gnathopod 2, segment 5 moderately expanded distally; segment 6 elongate, slender, tapering distally, palm short. Peraeopods 5 and 6, segments 4 and 5 subequal in length; peraeopod 7 segment 4 slightly shorter than 5. Coxal gills typical for genus. Epimeral plate 3, posterodistal tooth moderately stout. Uropod 1, peduncle with 4 longish, marginal spines. Uropod 2, peduncle and outer ramus, each with about 7 short spines. Uropod 3, inner ramus distinctly shorter than outer, both margins weakly spinose; outer ramus, outer margin with 4 or 5 spines. Telson lobes fused in basal  $\frac{1}{3}$ , inner margins rounded apically and bearing 1 or 2 apical spines.

Male. (penultimate instar 13.5 mm). Antenna 1, flagellum 21-segmented. Antenna 2, flagellum 36-segmented. Uropod 3 rami spinose and setose marginally.

*Distributional Ecology:* North Bering Sea, 25 m depth, to the Sea of Okhotsk and the Sea of Japan at depths of 45 m to 115 m. Ovigerous females in July.

*Remarks:* Material from the Bering Sea differs slightly from Gurjanova's description of *W. wirketis*. The rami of uropod 2 are spinose rather than smooth, and the rami of uropod 3 are unequal, not subequal.

The presence of a small lower antennal lobe, the well defined palm of gnathopod 1, and the 4 or 5 apical setae on the inner plate of maxilla 1

distinguish *W. wirketis* from the closely related *W. boreopacificus*. The narrow, acute eyelobe, and the elongate sixth segment of gnathopod 2 separate *W. wirketis* from *W. similis* n.sp., and *W. wecomus* (Barnard).

**Genus *Psammonyx* Bousfield 1973**

*Tmetonyx* Stebbing, 1906 (in part)

*Diagnosis:* Body slender, elongate. Eyes when present, small, subovate. Antenna 1 elongate; peduncular segment 1 long, cylindrical, slightly produced anterodistally, peduncular segments 2 and 3 not shortened; flagellum proximal segments not fused, accessory flagellum with several segments. Antenna 2 less than twice length of antenna 1. Antennae 1 and 2 calceolate (male); 1 and/or 2 not always calceolate (female). Mandible, molar strong; palp segment 1 usually with distal setae; segment 2 with mediobasal setae; segment 3 both margins setose. Maxilla 1, inner plate with 1 or 2 apical setae. Maxilla 2, inner plate slightly smaller than outer. Maxilliped,

outer plate short, not extending beyond palp segment 2; palp stout. Gnathopod 1 subchelate, palm well defined, dactyl strong. Gnathopod 2 minutely chelate or subchelate. Peraeopods 3 and 4, segment 4 strongly produced anterodistally; segment 6 with 2 short spines posterodistally. Coxa 4, posterodistal margin notched. Peraeopod 5 much shorter than 6 and 7, coxa equal to or deeper than segment 2; segments 4 and 5 expanded. Peraeopod 7 longest, lacking coxal gill. Epimeral plate 3 with or without a posterodistal tooth. Uropod 3 large, rami extending well beyond uropods 1 and 2, rami marginally spinose, and plumose. Telson lobes elongate, fused basally, weakly tapered, apices subtruncate, each with 2-5 spines.

*Type species:* *Anonyx nobilis* Stimpson, 1853

*Additional species:*

*P. terranova* Steele, 1978

*P. kurilicus* (Gurjanova) 1962

*P. longimerus* new species

**Key to Species of *Psammonyx***

- 1. Epimeral plate 3 with well developed posterodistal tooth; antenna 2 not calceolate in female; gnathopod 1, segments 5 and 6 moderately long, narrow ..... 2  
Epimeral plate 3, posterodistal tooth minute or lacking; antenna 2 calceolate in female; gnathopod 1, segments 5 and 6 short, broad ..... 3
- 2. Epimeral plate 3, posterodistal tooth with a dorsal notch; gnathopod 2, segment 5 elongate, slender, margins subparallel; uropod 3, segment 2 outer ramus minute ..... *P. longimerus* n.sp. (p. 118)  
Epimeral plate 3, posterodistal tooth lacking a dorsal notch; gnathopod 2, segment 5 relatively short, broadening distally, uropod 3, segment 2 outer ramus stout ..... *P. kurilicus* (Gurjanova)
- 3. Coxae 1 to 4, lower margins lined with setae; telson lobes each with 2 short apical spines; anterior head lobe moderately produced, rounded ..... *P. nobilis* (Stimpson)  
Coxae 1 to 4, lower margins bare; telson lobes each with 4 medium apical spines; anterior head lobe slightly produced, subacute ..... *P. terranova* Steele

***Psammonyx longimerus* n.sp.**

Figure 8.

*Material examined:* 48 specimens from 15 samples. Northern mainland coastal British Columbia: Bousfield stn. H59, off Bolivar Is. (15°35'N, 128°08'W), 14.5 m, 9 August 1964, holotype male (14.0 mm fig'd) NMC-1981-1057; allotype female ov. (14.0 mm) NMC-C-1981-1058, NMNS slide mounts, paratype male, 4 paratype female and 4 imm. paratypes, NMC-C-1981-1059; H62, head of River's Inlet (51°41'N, 127°15'W) 18-27 m, 10 August 1964. Southern mainland coastal British Columbia

and Vancouver Island: Bousfield stns. 1959; N6 Raynor Pt. (51°08'N, 127°41'W); V22 Oyster Bay (49°55'N, 125°11'W); 012 Ahous B., Vargas Is. (49°11'N, 126°01'W); 1964; H41 Jordan R. (48°25'N, 124°02'W); 1970; P703 McKenzie Beach (48°45'N, 125°15'W); 1975; P14 Keena Bay (48°47'N, 125°11'W); all collections intertidal. Washington, USA: Bousfield stns. 1966: W22 Pt. Grenville, Gray's Harbor Co. (47°18'N, 124°16'W); W36 Clallam Bay, Clallam Co., (48°15'N, 124°16'W); collections intertidal. Oregon: Coos Bay, (43°20'N, 124°30'W) 50-200 m, April 1979 to May 1980, coll. J. Trautman.



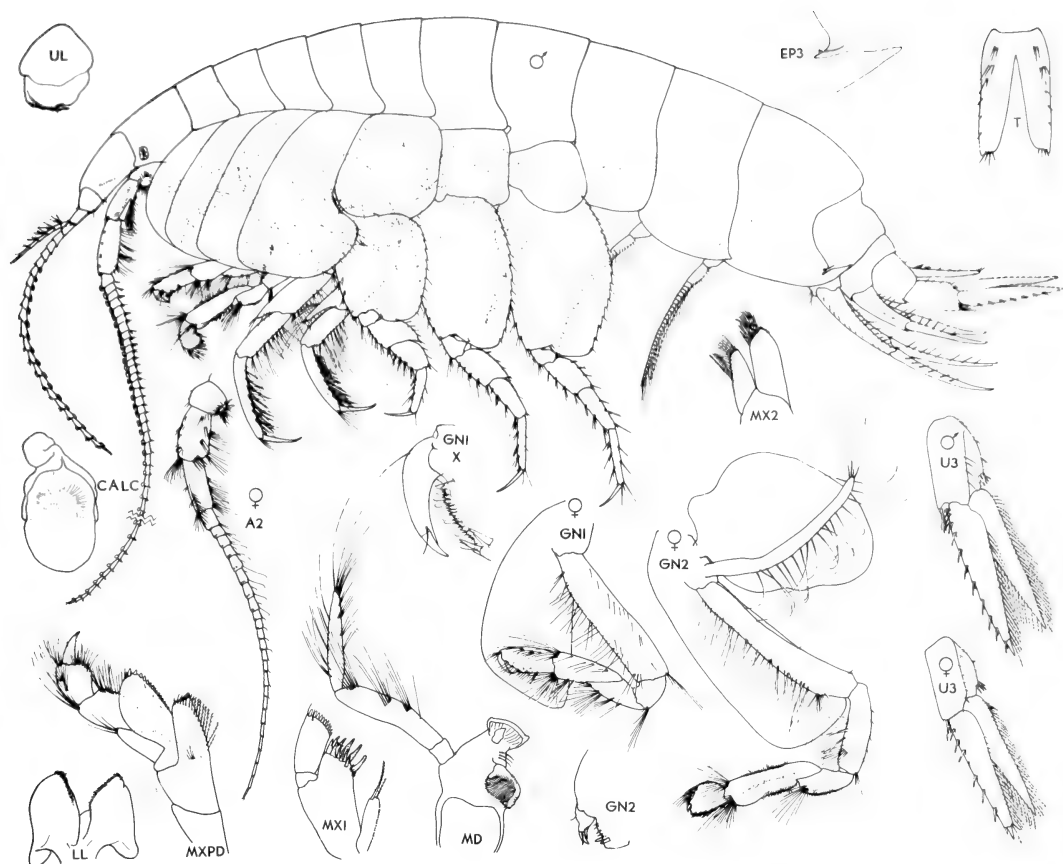


Figure 8. *Psammonyx longimerus* n.sp. Stn. H59, Bolivar I., B.C. ♂ 14 mm. ♀ 14 mm.

**Diagnosis:** Holotype male 14.0 mm. Anterior head lobe small. Eye small, indistinct in preserved specimens. Antenna 1 elongate, flagellar segments widest distally, distal margins fringed with short setae, and bearing setal tufts anteriorly and posteriorly; flagellum 23-segmented, calceolate; accessory flagellum 6-7 segmented, proximal segments distally with long setal tufts. Antenna 2, peduncular segments 4 and 5 with long posterior marginal setae; flagellum 37-segmented, calceolate. Mandible, palp segment 3 slightly shorter and more slender than segment 2, with 3 to 4 setal tufts on the outer and inner margins; segment 2 inner margin with 3-4 setal groups. Maxilla 1, palp broad with apical spine teeth in dense row, inner plate with 2 setae. Maxilliped, inner plate, apex transverse with 3 spine teeth. Gnathopod 1, segment 5 longer than 6; segment 6 narrow, palm slightly convex, distinctly shorter than posterior margin, dactyl barely exceeding palm. Gnatho-

pod 2, segment 5 elongate, margins subparallel; segment 6 short, broad, minutely subchelate. Peraeopod 3 anterodistal lobe of segment 4 overhangs one-third of segment 5; peraeopod 4, anterodistal lobe of segment 4 overhangs two-thirds the length of segment 5; segments 4, 5 and 6, posterior margin densely lined with long setal groups. Coxa 4, posterodistal margin with about 11 setal notches. Peraeopod 5, coxa as deep as segment 2. Peraeopods 6 and 7, segment 2 deep, posterior margin with strong notches and longish setae; peraeopod 7 distal margin of segment 2 straight. Peraeopods 5 to 7, anterior margin of segments 4 to 6 each with 4-5 groups of longish spines. Coxal gills on peraeopods 2, 3 and 4 simple, on 5 with 1, and on 6 with 3 accessory lobes; gill lacking on peraeopod 7. Epimeral plate 3 with a slender, tapering, posterodistal tooth, dorsal margin convex with a distinct notch bearing 1 short seta. Uropod 1,

peduncle and rami strongly spinose, spines longer and more numerous (about 8) on inner ramus. Uropod 2 peduncle with long, slender spines; lateral margin of outer ramus with short spines, inner ramus smooth. Uropod 3, rami elongate, narrowly tapering; inner ramus with both margins bearing plumose setae; outer ramus with inner margin bearing plumose setae, outer margin with 8 pairs of spines. Telson lobes fused only near base, each lobe with 3-4 dorsal spine groups, 2-4 single outer marginal spines, and 5 apical spines.

Female ov. (14.0 mm). Both antennae lack calceoli. Antenna 2 slightly longer than antenna 1; peduncle 5 with long anterodistal setae; flagellum 26-segmented; proximal segments with tufts of long setae posterodistally; all segments with short setal rows anterodistally.

**Distributional ecology:** From northern coastal British Columbia south to Coos Bay, Oregon, mainly on sandy bottoms from shoreline and shallows to 200 m in depth. Ovigerous females in July and August.

**Remarks:** The addition of *P. longimerus* n.sp. and the transfer of *H. kurilicus* Gurjanova to *Psammonyx* extends this previously Atlantic genus into the North Pacific region. Both Pacific species differ in having well developed posterodistal teeth on epimeral plate 3, longer, more slender segments 5 and 6 of gnathopod 1, and a shorter segment 6 of pereopod 7. These and other differences might justify separate sub-generic status for the Pacific species complex, but formal proposal awaits further study. *Psammonyx longimerus* is distinguished from *P. kurilicus* by the elongate article 5 of gnathopod 2, the pronounced anterodistal process of segment 4, pereopod 4, and the well developed dorsal notch on the third epimeral tooth.

### Genus *Paratryphosites* Stebbing, 1899

*Paratryphosites* Stebbing, 1906, p. 42

**Diagnosis:** Body elongate. Head relatively broad; anterior head lobe small. Eyes (in alcohol) medium large, oval. Antenna 1 peduncular segment 1 slightly produced anterodistally; segments 2 and 3 telescoped; flagellum short in the female and elongate in the male; accessory flagellum multiarticulate. Antenna 2 flagellum very elongate in the male, terminal segments very long and thin. Antennae 1 and 2 calceolate in male. Mandible, palp segments 2 and 3 subequal; segment 3 inner margin with comb setae; molar

massive. Maxilla 1, inner plate with 5 apical setae. Maxilliped, inner plate short, not extending beyond segment 2 of palp, margins of apices concave. Gnathopod 1, segment 5 longer than 6; segment 6 palm oblique, well defined. Gnathopod 2, subchelate. Pereopod 5 not shortened; pereopods 5, 6 and 7, segment 2 with posterior margins coarsely serrate; pereopod 6 longest. Epimeral plate 3 produced in an upturned posterodistal tooth. Pereopods 2, 3 and 4 with simple coxal gills; P5 gill with one, P6 with 2 accessory lobes, pereopod 7 coxal gill lacking. Uropod 3 rami foliaceous (♂). Telson short, broad, lobes fused  $\frac{1}{2}$ ; apices broadly truncate, each with 7-9 spines.

**Type species:** *Paratryphosites abyssi* (Goes, 1866),

### *Paratryphosites abyssi* (Goes, 1866)

*Lysianassa abyssi* Goes, 1866, p. 519, plate 37, fig. 5.

*Paratryphosites abyssi* — Shoemaker, 1930, p. 18, fig. 10 (♂ - ?)

*Hippomedon abyssi* — Gurjanova (1962) p. 126-132, figs. 32a, b, 33a, b

**Material examined:** 100+ specimens (♂♂, 13 mm - 16 mm.), Gulf of St. Lawrence, Laurentian Trench, 300 m, July 1969. Coll: Marine Sciences Centre, McGill University, Montreal. 1 ♀ ovigerous (13 mm.) Entrance to Baie des Chaleurs, stn. HP112M (48°18'07"N, 64°21'22"W), 119 m., 26 June 1969, coll: P. Brunel.

**Remarks:** In *Paratryphosites abyssi* the flagellum of antenna 1 in the female is approximately 12 segmented, whereas it is approximately 30 segmented in the male. This sexually dimorphic character of the first antenna is unique among all the genera included in this study. Based on the relative lengths of the antennae Shoemaker (1930) has figured a female rather than a male. Unfortunately, the size of the specimen figured was not given and the single specimen has not been re-examined. Coxal gills were lacking on pereopod 7 in all specimens.

Through the courtesy of Dr. Pierre Brunel we reproduce herewith a description of the colour present in a mature male taken from a specimen about a week after capture, the specimen having been preserved in 4% formaldehyde. "The eyes, which have never been observed or figured so far, were orange red, and so were three oblique lateral stripes on the metasome, which may be

muscle insertions. Whole animals were otherwise whitish."

## Addendum

Material of the following species, from Gurjanova's original localities in the far eastern seas of the USSR, has very recently been made available to us through the courtesy of Dr. Nina Tzvetkova, Zoological Museum, Leningrad:

*Hippomedon wirketis* (Gurjanova 1962) — ♀  
br. II Kurile Straits

*Hippomedon kurilicus* (Gurjanova 1962 — ♂  
and ♀ specimens, N. Kuriles.

*Hippomedon pacificus* Gurjanova 1962 — ♂  
and ♀ — Okhotsk Sea

*Hippomedon minusculus* Gurjanova 1938 — 4  
♀ ♀ — S. Kuriles.

*Hippomedon propinquus eous* Gurjanova 1962  
— ♂ ♂ and ♀ — Okhotsk Sea.

*Hippomedon denticulatus orientalis* Gurjanova  
1962 — ♂ & ♀ — Shikotan I.

*Hippomedon punctatus* Gurjanova 1962 — ♂  
and ♀ — N. Kurile Islands.

The specimens of *H. pacificus*, *propinquus eous*, and *punctatus* fairly closely match the descriptions and illustrations of Gurjanova (1962). However, some discrepancies were noted when comparing the specimens of *H. wirketis*, *kurilicus*, *minusculus*, and *d. orientalis* with the original descriptions and illustrations. In these instances, the specimens were apparently not from the type localities but from distributional localities of the original text. The possibility that Dr. Gurjanova's original material concealed greater taxonomic diversity than described in her very fine and comprehensive monograph (1962) would merit further investigation.

## Discussion

A character analysis was carried out on 21 species of *Hippomedon* (sens. lat) and 2 species of *Psammonyx* using numerical taxonomical methods (Sneath & Sokal, 1973). Specimens were unavailable for the following eleven species (character data from litt. only): *H. minusculus* Gurj. (Sea of Japan), *H. punctatus* Gurj. (Sea of Okhotsk), *H. kurilicus* Gurj. (Sea of Okhotsk, Bering Sea), *H. pacificus* Gurj. (Kuriles), *H. denticulatus orientalis* Gurj. (Chuckchi and Bering Seas), *H. coecus* (Holmes) (California), *H. subrobustus* Hurley (California), *H. zetesimus* Hurley

(California) and *H. tenax* Barnard (California).

Owing to limitations imposed by the literature, the analyses were restricted to twenty-three characters considered to be of generic value. Character states were assigned values of 0 = primitive or plesiomorphic, .5 = intermediate, 1 = advanced or apomorphic (Table 1), and a raw data matrix compiled therefrom (Table 2). In this analysis, advanced species would have high total scores, primitive species would have low total scores. The similarity coefficient used to calculate the similarities between all pairs of species was that of Rogers and Tanimoto. (Sneath & Sokal 1973, p. 132) and formed the basis for the similarity matrix of Table 3. The clustering technique used to define clusters of mutually similar taxa was that of Complete Linkage Clustering (Sneath & Sokal 1973, p. 222) from which the phenogram (fig. 9) was constructed.

This phenogram reveals four species groupings having an overall dissimilarity of 50% or greater in 23 selected characters. Differences of such magnitude between these groupings confirms the validity of the existing generic concepts of *Hippomedon* Boeck (*Sens. Str.*), and *Psammonyx* Bousfield, the re-establishment of *Paratryphosites* Stebbing as a separate genus and creation of the new genus *Wecomedon* herewith.

These four generic groups are quite unequal in number of species and in relative plesiomorphy-apomorphy. Thus, in the north Pacific region, *Hippomedon* (*Sens. Str.*) is by far the largest group with 13 species, all relatively apomorphic (values of .57 - .85); *Wecomedon* is next largest with 5 known species, of medium apomorphy (values of .45 - .50); *Psammonyx* is yet smaller, with two Pacific species, of greatest plesiomorphy (values of .30 - .35), whereas the monotypic *Paratryphosites* of holarctic and North Atlantic affinities (not yet actually recorded from the North Pacific) contains only one species, of intermediate apomorphy (value of .57).

The general correlation between the range of plesiomorphy-apomorphy values and the pertinent species groupings tends to confirm these genera as "natural" rather than "artificial" or convergent.

The temptation is strong to carry this analysis to subgeneric levels (at 50-75% similarity levels). Thus, within *Psammonyx*, some justification might be found for formal subgeneric recognition of the Pacific *longimerus* and *kurilicus* from the Atlantic *nobilis* and *terranae* on the basis

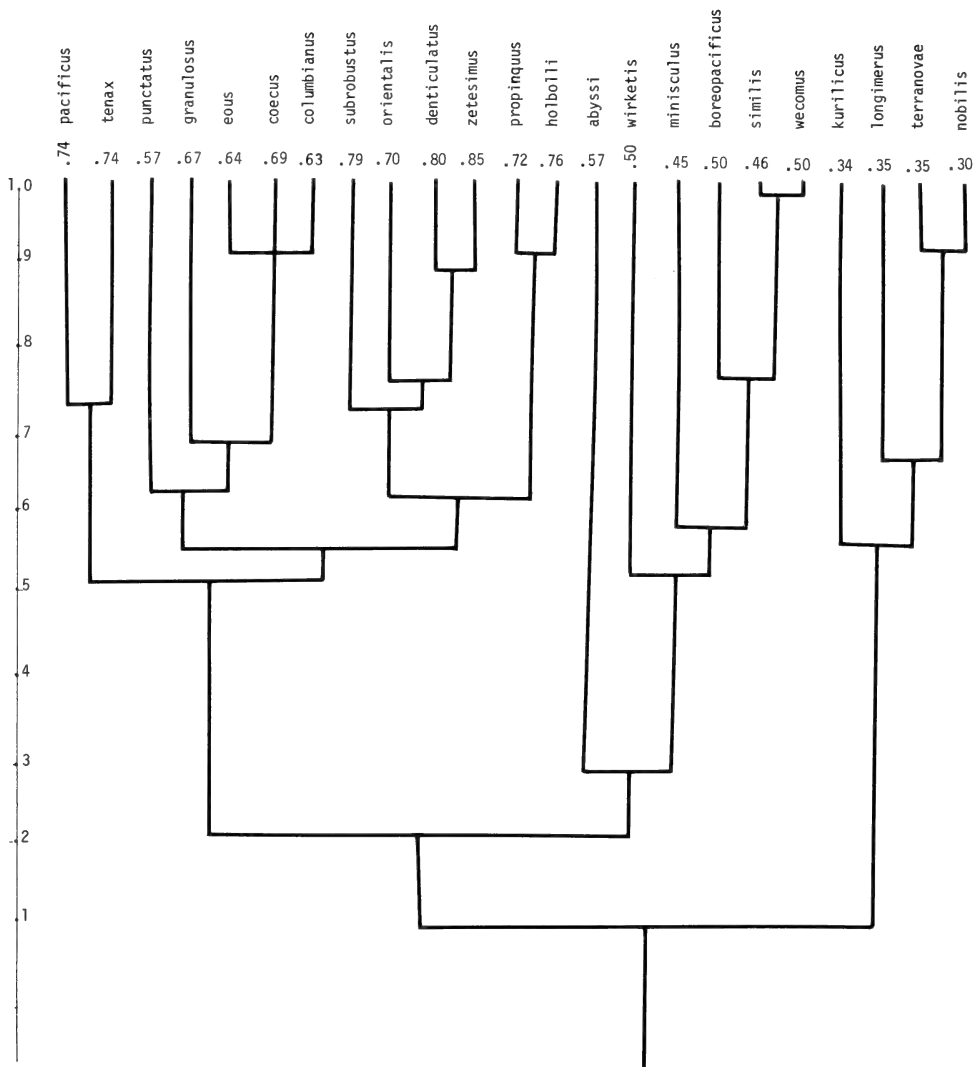


Figure 9. Phenogram of species and genera of *Hippomedon* sens. lat. complete linkage cluster analysis. Number beside each species is index of apomorphy.

of their prominent epimeral 2 tooth, less fossorial peraeopod 5, lack of antennal calceoli in the ♂, etc. Such temptation must be resisted in the much more diverse genus *Hippomedon* since only a small fraction of known world species are represented in the Pacific regional fauna. Despite their relative overall apomorphy, all members of *Hippomedon* retain some plesiomorphic characters such as calceolate antennae (♂), and the presence of coxal gills on peraeopod 7. A literature review of additional species showed that the Atlantic species exhibit the most advanced form of the first gnathopod, the palm becoming so

indistinct that it is almost simple (*H. serratus*), and also of the anterodistal process of antenna 1 which is more pronounced (*H. denticulatus*, *H. nasutus*, *H. serratus*) than in any of the Pacific species. Many species of *Hippomedon* previously thought to be lacking eyes have proven to have eyes of a pigmentary type which disappear completely after preservation. Descriptions of eyes within this genus should be based on animals which have been studied in the living condition (Vader 1968). A more primitive condition exists in *H. holbolli* previously known to have a crystalline eye lens in preserved specimens and

now known to have an additional large pigmentary component which is visible in live specimens (J. Just pers. comm). This eye type was also described by Bellan-Santini (1965) for *H. massiliensis* from the Mediterranean. Preserved specimens of *H. gorburnovi* and *H. rylovi* from the Arctic have crystalline eye lenses. However, formal recognition of other supraspecific groups awaits a more comprehensive study of the world fauna.

The five species presently comprising the new genus *Wecomedon* are less advanced than those of *Hippomedon* in most respects, except for the loss of the coxal gill on pereopod 7 and apparent incipient loss of the calceoli on the male antenna. Analysis is hampered by a scarcity of mature males in the collections, but in the single calceolate male specimen available, the number of calceoli was reduced to 3. The relatively small spread of character indices (.46 - .50) suggests a relatively tightly knit complex of species of relatively low diversity as compared to the genus *Hippomedon*. The peduncle of antenna 1 has a less expanded first segment, and segments 2 and 3 are less telescoped. The proximal flagellar segments are not fused, and although segment 1 is slightly longer than the following segments, it is always much shorter than the accessory flagellum. Antenna 2 (♀) is not much longer than antenna 1, and the weakly tapered telson lobes with multiple apical spines are also primitive. *Wecomedon* appears intermediate in almost every respect between the apomorphic genus *Hippomedon* and the plesiomorphic genus *Psammonyx*.

*Psammonyx* as the most primitive of the genera

analyzed. The antennae, uropods and telson are especially plesiomorphic (see Table 1). On the other hand, the fifth pereopod is highly specialized and fossorial in function.

The posterodistal tooth of epimeral plate 3, rudimentary in the Atlantic species, is developed to a much greater extent in their Pacific counterparts.

In gnathopod 1 of the Pacific species, the coxa is not reduced and segments 5 and 6 are longer and more slender, and segment 6 of pereopod 7 is not as long as in Atlantic species. Both groups possess setose mandibular palps, the setose third uropods, and the long, deeply cleft, multi-spined telson, all primitive characters.

The monotypic *Paratryphosites*, having an intermediate character index of .57, exhibits characters present to some extent in each of the other genera but in a combination that is unique to this genus. In addition, the short broad telson, cleft less than half-way, the massive flat mandibular molar, the shortened article 5 of gnathopod 2 and the sexually dimorphic antennae are not found in any other genera.

Future analysis of the remaining lysianassid material from the Canadian Pacific coastal areas will hopefully provide insights into taxonomic relationships which exist between these genera and others. Hopefully also, the true nature and significance of geographical differences between populations and between species and genera will be revealed through more extensive collections both geographically and bathymetrically and more extensive application of analytical methodology.

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**Table 1. Data matrix showing character state as defined in Table 2 of North Pacific and selected North Atlantic species of *Hippomedon* (sens. lat.)**

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	P.A. Index
<i>Ps. nobilis</i>	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1	0	0	0	1	0	.30
<i>Ps. kurilicus</i>	0	0	0	0	0	.5	0	NC	0	1	0	1	0	0	.5	.5	1	1	1	0	0	1	0	.34
<i>Ps. longimerus</i>	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	1	0	.35
<i>Ps. terranova</i>	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1	0	1	0	1	0	.35
<i>W. minusculus</i>	0	0	0	1	0	1	NC	NC	NC	1	0	.5	0	0	.5	0	0	1	1	.5	1	1	.5	.45
<i>W. similis</i>	.5	0	0	.5	0	1	0	0	1	1	0	1	0	1	.5	.5	0	1	1	0	.5	1	0	.46
<i>W. wirketis</i>	.5	0	0	0	0	1	NC	1	1	0	0	1	0	1	.5	.5	0	1	1	0	.5	1	0	.50
<i>W. boreopacificus</i>	.5	0	0	0	0	1	NC	NC	NC	1	0	1	.5	1	.5	.5	0	1	1	.5	.5	1	0	.50
<i>W. wecomus</i>	.5	0	0	.5	0	1	NC	0	1	1	0	1	0	1	.5	.5	0	1	1	.5	.5	1	0	.50
<i>Pa. abyssi</i>	.5	1	0	1	1	1	0	1	1	0	0	1	.5	1	1	0	0	1	1	0	0	1	0	.57
<i>H. punctatus</i>	.5	1	1	1	1	1	0	NC	1	0	0	1	0	0	1	0	1	0	1	0	1	0	1	.57
<i>H. columbianus</i>	.5	1	1	1	1	1	0	1	1	0	0	1	0	0	.5	0	1	0	1	.5	1	1	1	.63
<i>H. eous</i>	.5	1	1	1	1	1	0	NC	1	0	0	1	0	0	1	0	1	0	1	.5	1	1	1	.64
<i>H. granulosus</i>	.5	1	1	1	1	1	0	1	1	.5	0	1	.5	0	1	0	1	0	1	.5	1	1	.5	.67
<i>H. coecus</i>	.5	1	1	1	1	1	0	NC	1	1	0	1	0	0	.5	0	1	NC	1	.5	1	1	1	.69
<i>H. orientalis</i>	.5	1	1	1	1	1	0	NC	1	1	0	1	.5	1	1	0	1	0	1	.5	1	0	1	.70
<i>H. propinquus</i>	.5	1	1	1	1	1	0	1	1	1	0	1	1	0	1	0	1	0	1	0	1	1	1	.72
<i>H. pacificus</i>	.5	1	1	1	1	1	NC	NC	1	.5	0	1	.5	0	1	.5	1	0	1	.5	1	1	1	.74
<i>H. tenax</i>	0	1	1	1	1	1	NC	NC	NC	1	0	.5	.5	0	1	.5	1	NC	1	.5	1	1	1	.74
<i>H. holbolli</i>	.5	1	1	1	1	1	0	1	1	1	0	1	1	0	1	0	1	0	1	1	1	1	1	.76
<i>H. subrobustus</i>	NC	1	1	1	1	1	0	1	1	1	0	1	.5	1	1	0	1	NC	1	0	1	1	1	.79
<i>H. denticulatus</i>	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	1	0	1	.5	1	1	1	.80
<i>H. zetesimus</i>	.5	1	1	1	1	1	NC	1	1	NC	0	1	1	1	1	0	1	NC	1	.5	1	1	1	.85

P.A. Index is the index of plesiomorphy vs. apomorphy. The higher the number the more advanced the character states.

State 0 = Character primitive (plesiomorphic)

.5 = Character intermediate

1 = Character advanced (apomorphic)

NC = No comparison, missing data



**Table 2. Qualitative Multistate Characters**

1. A <sub>1</sub> ped. seg.1 anterodistal process well developed	1	13. Gn <sub>1</sub> palm oblique, not well defined	1
absent	0	palm transverse, defined	0
2. A <sub>1</sub> ped. seg. 1 short, well inflated, segs. 2 & 3 short	1	14. Gn <sub>2</sub> palm short	1
A <sub>1</sub> ped. seg. 1 long, weakly inflated, segs. 2 & 3 long	0	palm long	0
3. A <sub>1</sub> main flag. proximal segs. conjoint	1	15. P <sub>3</sub> and 4 dactyls long	1
segs. distinct not conjoint	0	dactyls moderate	0
4. A <sub>1</sub> main flag. short	1	16. P <sub>5</sub> shortened, coxa as deep as seg. 2	1
elongate	0	not shortened, coxa not as deep as seg. 2	0
5. A <sub>2</sub> more than twice length A <sub>1</sub>	1	17. P <sub>7</sub> seg. 2 tapered	1
less than twice length A <sub>1</sub>	0	not tapered	0
6. A <sub>2</sub> flag. segs. simple	1	18. Gill absent, P <sub>7</sub>	1
well developed	0	present, P <sub>7</sub>	0
7. Antennae not calceolate	1	19. Epimeral sideplate 3 with a well-developed tooth	1
calceolate	0	sideplate 3 without a well-developed tooth	0
8. Mandibular palp seg. 1 without distal setae	1	20. U <sub>1</sub> and U <sub>2</sub> , ped. and rami mainly smooth	1
with distal setae	0	mainly spinose	0
9. Mandibular palp seg. 3 comb setose medially	1	21. U <sub>3</sub> rami spinose	1
not comb setose (other setation)	0	rami setose	0
10. Mx <sub>1</sub> inner plate 2 setae apically	1	22. U <sub>3</sub> rami margins tapered throughout length	1
more than 2 setae apically	0	rami margins parallel, tapered only at tips	0
11. Coxa 1 reduced	1	23. Telson lobes well tapered, 1 spine apically	1
not reduced	0	lobes weakly tapered, multiple spines apically	0
12. Gn <sub>1</sub> seg. 5 greater than 6	1		
seg. 6 greater than 5	0		

**Table 3. Similarity Matrix**

Species		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W
nobilis	A	X																						
terranovae	B	.92	X																					
longimerus	C	.70	.64	X																				
kurilicus	D	.57	.52	.63	X																			
abyssi	E	.31	.28	.31	.33	X																		
wirketis	F	.21	.21	.28	.31	.39	X																	
minusculus	G	.40	.40	.56	.54	.26	.40	X																
wecomus	H	.38	.38	.38	.50	.42	.52	.56	X															
similis	I	.39	.39	.39	.52	.44	.48	.56	1.0	X														
boreopacificus	J	.29	.29	.38	.38	.29	.60	.73	.74	.74	X													
holbolli	K	.09	.12	.15	.19	.31	.24	.31	.26	.28	.25	X												
denticulatus	L	.15	.15	.21	.18	.35	.24	.35	.29	.31	.33	.70	X											
propinquus	M	.15	.12	.21	.26	.39	.24	.26	.26	.28	.29	.92	.77	X										
columbianus	N	.12	.12	.18	.26	.35	.35	.35	.33	.35	.38	.70	.64	.70	X									
granulosus	O	.09	.09	.15	.18	.39	.28	.26	.26	.28	.29	.64	.64	.70	.70	X								
pacificus	P	.11	.11	.14	.17	.33	.27	.25	.35	.38	.29	.62	.68	.62	.68	.68	X							
eous	Q	.10	.10	.13	.22	.29	.29	.33	.35	.33	.38	.63	.57	.63	.91	.69	.66	X						
orientalis	R	.15	.15	.16	.16	.38	.22	.29	.31	.34	.33	.69	.76	.69	.63	.69	.75	.62	X					
punctatus	S	.15	.11	.19	.22	.38	.27	.21	.31	.31	.33	.55	.73	.76	.76	.63	.62	.86	.69	X				
coecus	T	.24	.24	.33	.29	.35	.31	.41	.38	.40	.38	.62	.62	.68	.91	.83	.58	.90	.60	.66	X			
zetesimus	U	.13	.13	.21	.43	.43	.25	.36	.33	.33	.33	.74	.90	.82	.74	.74	.81	.73	.81	.65	.66	X		
subrobustus	V	.16	.16	.24	.21	.45	.20	.36	.29	.27	.29	.62	.75	.75	.63	.68	.73	.54	.74	.60	.54	.80	X	
tenax	W	.09	.09	.15	.23	.36	.19	.33	.27	.27	.24	.52	.58	.58	.58	.65	.73	.58	.58	.52	.52	.58	.64	X

**Table 4. Distribution of North American Pacific and Western Arctic species of *Hippomedon sens. lat.***

	Beaufort Sea	Bering Sea	South- Eastern Alaska	North B.C. Q.C.I.	Central B.C. & V.I.	Wash- ington	Oregon	Other
Paratryphosites abyssi	X	X	O	O	O	O	O	N. Atlantic Beaufort Sea Chuckchi Sea
Hippomedon holbolli	X	X	O	O	O	O	O	N. Atlantic Circumpolar
Wecomedon wirketis	O	X	O	O	O	O	O	Sea of Okhotsk Sea of Japan
Hippomedon granulosus	O	X	O	O	O	O	O	Sea of Okhotsk Sea of Japan
Wecomedon similis	O	X	-	X	O	O	O	
Wecomedon wecomus	O	O	X	-	X	X	X	
Hippomedon columbianus	O	O	O	X	X	O	O	
Psammonyx longimerus	O	O	O	O	X	X	X	

X present in samples examined

O not present in samples or in litt.

- no suitable samples from region



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